THE INFLUENCE OF INOCULUM DENSITY OF VESICULAR-ARBUSCULAR MYCORRHIZAL FUNGI ON THEIR DEVELOPMENT AND ON FUSARIUM WILT OF TOMATO

BY

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Greenhouse investigations were conducted on the influence of vesicular-arbuscular mycorrhizae on the development of Fusarium wilt of tomato (Lycopersicon esculentum) and on the relationship of inoculum density (ID) of mycorrhizal fungi to their development and to tomato growth response. Chlamydospores of Glomus etunicatum or G. mosseae were mixed with autoclaved sandy soil (< 30 µg phosphorus/g) to achieve 0.0, 0.1, 0.3, 0.5, 0.7, 1.0, and 10.0 chlamydospores per gram of soil (cpg). Chlamydospores of Fusarium oxysporum f. sp. lycopersici race 2 (Fol) were mixed with mycorrhizal fungus-infested or noninfested autoclaved soil to achieve 500 cpg. Seeds or 2-wk-old transplants (grown in noninfested soil or in mycorrhizal fungus-infested soil) of the wilt-susceptible tomato cultivar Manapal were planted in Fol-infested or noninfested soil. After 20 days chlorosis and wilt were observed on plants grown in soil infested with either mycorrhizal fungus and Fol but were not observed on plants grown in soil infested with Fol alone until after 30 days. Disease onset

was similar regardless of the inoculum level or species of the mycorrhizal fungus tested, or of plant age at the time of exposure to inoculum of Fol. In the disease interaction study, development of mycorrhizae was restricted to individual sites of fungus root colonization and the effects of mycorrhizae on plant growth were inconsistent. By 6-8 wk disease severity (DS) was reduced significantly ($P < 0.01$) in the presence of the mycorrhizal fungi and Fol from plants grown in soil infested with Fol alone. Phosphorus amendments to plants grown in soil infested with Fol alone lessened DS. Thus DS was least with Fol plus phosphorus, intermediate with either mycorrhizal fungus plus Fol, and greatest with Fol alone. Statistically significant linear and quadratic relationships were detected between ID and mycorrhizal fungus root colonization, a colonization index (root weight factored in with percent colonization), or individual colonization sites for both mycorrhizal fungus species, although specific levels of colonization varied by species. Glomus mosseae colonized roots to a significantly greater ($P < 0.01$) extent than G. etunicatum.

GENERAL INTRODUCTION

The quantitative development of vesicular-arbuscular mycorrhizal fungi, utilizing levels of spore inoculum typical in field conditions, and the subsequent plant growth response have not been reported. A relationship between increasing inoculum density (ID) and fungus development or plant growth could influence the nature of mycorrhizae research by refining the methodology employed for experimentation. Disease interaction studies involving mycorrhizal fungi and plant pathogens have not been investigated quantitatively using spore inoculum of the mycorrhizal fungi. The magnitude of effects the mycorrhizal fungi have in the presence of a plant pathogen both on disease progression and on the pathogen are important aspects of understanding the ecology of the mycorrhizal fungi.

The objectives of this research were 1) to develop methods for distributing spore inoculum of the mycorrhizal fungi and the pathogen to simulate distribution under typical field conditions; 2) to evaluate the quantitative relationship between ID and fungus development or plant growth; and 3) to utilize this information to investigate the quantitative effects of mycorrhizal fungi on fungus development or plant growth in disease interactions involving a plant pathogen.

PART 1

THE DEVELOPMENT OF FUSARIUM WILT OF TOMATO AS INFLUENCED BY THE VESICULAR-ARBUSCULAR MYCORRHIZAL FUNGI, GLOMUS ETUNICATUM AND G. MOSSEAE

Introduction

Vesicular-arbuscular (VA) mycorrhizal fungi are ubiquitous and may benefit plant growth, especially in soils of low fertility, by increasing uptake of phosphorus, copper, zinc, and certain other minerals (Gerdemann, 1975; Lambert et al., 1979). Tomato (Lycopersicon esculentum Mill.) plants inoculated with a number of mycorrhizal fungi, including Glomus etunicatum Becker & Gerd. and G. mosseae (Nicol. & Gerd.) Gerd. & Trappe have improved growth compared with noninoculated plants (Daft and Nicolson, 1969, 1972; Daft and Okusanya, 1973a, 1973b; Gaunt, 1978; McGraw and Schenck, 1980, 1981; Sanni, 1976). In one study, mycorrhizal tomato plants possessed greater amounts of vascular stem tissue and greater lignification of secondary stem tissue than nonmycorrhizal plants (Daft and Okusanya, 1973b). Daft and Nicolson (1969, 1972) observed a positive relationship in tomato between increasing numbers of chlamydospores (ranging from 3 to 225 spores per plant of G. mosseae) and shoot height, length of leaves, or the number of leaves retained per plant, and between shoot dry weight and percent colonization with Endogone sp. [Glomus].

The growth benefits achieved by a mycorrhizal plant may be counteracted or reduced by the activity of plant pathogens. Schenck and Kellam

(1978) indicated that results of the majority of disease interaction studies can be interpreted as indicating that mycorrhizal plants may compensate for the damage caused by a pathogen, thus reducing disease severity (DS). Two reports on the influence of mycorrhizae on vascular wilt diseases have provided contrasting results. Increased wilt was observed in cotton inoculated with G. fasciculatum and Verticillium dahliae at 20 µg but not at 300 µg of superphosphate per g of soil as compared with nonmycorrhizal plants inoculated with V. dahliae (Davis et al., 1979). Dehne (1977) and Dehne and Schönbeck (1975) reported that tomato (L. lycopersicum (L.) Karst. Farw. = L. esculentum Mill. 'Rheinglut') plants preinoculated with G. mosseae followed by a later inoculation with Fusarium oxysporum Schlecht. f. sp. lycopersici (Sacc.) Snyd. & Hans. had decreased wilt compared with noninoculated plants. There have been no reports comparing the effects of different species of mycorrhizal fungi on the same wilt disease.

Fusarium wilt is one of the most researched diseases of tomato (Walker, 1971). Genetic resistance for control of the disease is available (Bohn and Tucker, 1940; Crill et al., 1972; Stall and Walter, 1965), although certain environmental conditions may weaken the resistance (Jones and Woltz, 1969; Retig et al., 1967). The nutritional status of both plant and soil may predispose plants to Fusarium wilt. Jones and Woltz (1972) found that high levels of superphosphate resulted in increased DS, and they speculated that this was due to a stimulation of the activity of the pathogen by micronutrients contained in the phosphate fertilizer.

Relationships between inoculum density (ID) and disease incidence (DI) in a plant population or DS have been found for several soilborne

fungal plant pathogens (Baker, 1971; Ferriss, 1982). Similar relationships between ID and fungus root colonization or plant growth may occur for VA mycorrhizal fungi. At propagule levels less than 0.5 per gram of soil, Smith and Walker (1981) found a linear relationship between ID of indigenous mycorrhizal fungi in nonsterile soil and the number of entry points by the fungi in Medicago trunculata roots. Saturation of entry points occurred above 0.5 propagule per gram of soil. Varying the levels of root colonization by mycorrhizal fungi by varying ID could influence the activity of an invading plant pathogenic fungus and hence influence the disease development.

The objectives of this study were 1) to ascertain the influence of ID of mycorrhizal fungi on the development of Fusarium wilt of tomato and on plant and fungus growth, and 2) to evaluate the effect of the length of time plants were exposed to either of two mycorrhizal fungi, Glomus etunicatum and G. mosseae, preceding inoculation with the wilt fungus on the same parameters. Additionally comparative effects of differing environmental conditions between this study and those of Dehne (1977) and Dehne and Schönbeck (1975) on Fusarium wilt were planned.

Materials and Methods

Two isolates of VA mycorrhizal fungi were used: an isolate of G. etunicatum obtained originally from J. W. Gerdemann, University of Illinois, and an isolate of G. mosseae obtained from N. C. Schenck, University of Florida. Chlamydospores used were produced in pot cultures (Mosse, 1953) of bahiagrass (Paspalum notatum Flügge) and were stored at 5 C until used in soil dried to approximately 2% moisture content. Inoculum was collected and concentrated by decanting and wet-sieving (Gerdemann and Nicolson, 1963) using an 88-µm-mesh sieve, and by centrifuging at 1270 x g in deionized water for 3 min and in chilled 2 M sucrose for 1.5 min. Spores were rinsed in deionized water immediately after the last centrifugation and then were resuspended in deionized water. The number of chlamydospores per milliliter of suspension was evaluated using a dissecting microscope (20 X) by counting spores contained in ten 0.1-ml aliquots.

The isolate of F. oxysporum f. sp. lycopersici race 2 (Fol) used was isolated originally from diseased tomato in 1977, and was obtained from J. P. Jones, University of Florida Agricultural Research and Education Center, Bradenton. The culture was stored in a sterilized mixture of soil and sand (1/1, v/v) at 5 C. Chlamydospores were produced in sterile soil-extract water by a modification of the method by Alexander and coworkers (1966). Autoclaved soil-extract water (one kilogram of a field soil [Lakeland fine sand] per liter of tap water; autoclaved 1 hr at 121 C and 1.1 kg/cm^2) was vacuum-filtered through a double layer of Whatman no. 4 filter paper. Cultures for the production of chlamydospores were initiated by adding one 3-mm-diameter agar plug from a 2-wk-old culture of Fol grown on potato dextrose agar to 85 ml of sterile

soil-extract water in 250-ml flask. Mats of chlamydospores formed after 2 wk of incubation at 25 C in the dark were removed, disrupted by homogenizing with a glass tissue grinder, and sonicated for two 20-sec intervals at 400 W with a Bronsonic 1510 sonicator (B. Braun Instruments, San Francisco, CA 94080). The resulting suspension was centrifuged at 1270 x g for 3 min and the pellet containing the spores was resuspended in sterile deionized water. The number of chlamydospores per milliliter of suspension was estimated by counting five fields for each of five samples on a standard hemacytometer.

Lakeland fine sand (192-256 µg Ca/g; 0.36-0.92 µg Cu/g; 9.2-9.6 µg Fe/g; 32.0-48.0 µg K/g; 22.1-48.0 µg Mg/g; 14.0-30.0 µg Mn/g; 34.2-45.0 µg PO_4/g; and 6.2-6.3 pH, as analyzed by the Soils Clinic, University of Florida) that had been autoclaved (121 C at 0.7 kg/cm^2) for two 4-hr periods separated by a 24-hr interval and aged for 1 wk was infested with either G. etunicatum or G. mosseae, the wilt fungus, each mycorrhizal fungus plus the wilt fungus, or was not infested. The autoclaved soil was infested and mixed to achieve an initial inoculum level of 0.0, 0.1, 0.5, and 10.0 chlamydospore per gram of soil (cpg) of the two mycorrhizal fungi and 500 cpg of the wilt fungus. The inoculum levles selected for the mycorrhizal fungi are thought to be reflective of typical densities of spore populations in agricultural soils (McGraw and Hendrix, unpublished; Schenck and Kinloch, 1980). The wilt fungus was infested at 500 cpg based on results from a preliminary experiment (reported in Appendix 4 of this dissertation) and reports in the literature for similar fungi (Guy and Baker, 1977).

Two kilograms of autoclaved soil infested with either mycorrhizal fungus or the wilt fungus were mixed for 2 min at low speed in a Hobart benchtop food mixer (Hobart Co., Troy, OH 45374), then mixed with a larger

volume of treated soil for 5 min in a portable cement mixer. Mixers were alcohol-flamed between dissimilar treatments. Soil not infested with mycorrhizal fungi (0.0 cpg) received filtered washes from the centrifuged chlamydospores of these fungi. Two kilograms of infested or noninfested soil were added per 15-cm-diameter plastic pot.

The length of time plants were exposed to inoculum of each mycorrhizal fungus was evaluated in two types of experiments. In one type of experiment (transplants), three surface-disinfected (10 min in 0.525% sodium hypochlorite with three rinses in sterile deionized water) seeds of the tomato cv. Manapal (resistant to race 1 and susceptible to race 2) were seeded in soil in 50-ml plastic beakers and thinned within 1 wk to one plant per container. Soil in the beakers was either noninfested (receiving filtered spore washes from the spore suspension of each mycorrhizal fungus) or infested with G. etunicatum or G. mosseae at 0.1, 0.5, and 1.0 cpg. Two weeks after seeding, the seedlings (with soil from each container) were transplanted to similarly infested soil in 15-cm-diameter plastic pots. The wilt fungus was added at 500 cpg simultaneously with inoculum of the mycorrhizal fungi to the larger volume of soil or else was added alone to the soil. In a second type of experiment (seeds), three surface-disinfected Manapal seeds were planted per 15-cm-diameter plastic pot in noninfested soil receiving spore-wash water or were planted immediately following infestation of soil with the mycorrhizal fungi or with Fol in the same treatments used in the transplant experiment. Seedlings were thinned within 1 wk to one plant per pot. Experiments were conducted during the months of September to January (1980-81). Plants were maintained in a greenhouse with air temperatures ranging from 22-30 C and were watered daily. Plants not inoculated

with a mycorrhizal fungus were fertilized (50 ml/ pot/ wk) with 2X Hoagland's solution (Hoagland and Arnon, 1938) with or without phosphorus (PO_4). Plants inoculated with a mycorrhizal fungus received 50 ml of 2X Hoagland's solution minus PO_4 per pot weekly.

Each experiment was conducted twice. Plants were examined daily after inoculation to detect the time of symptom onset. Five plants in each treatment for each of the two types of experiments were sacrificed for evaluation 6 and 8 wk after inoculation; thus a total of eight evaluation dates occurred. The procedures for each evaluation date were as follows: prior to removal of plants from soil, shoot height was measured and above-ground disease severity was estimated using an index of 0-4, where 0 = no symptoms, 1 = 1-25% of the shoot with symptoms, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%. Disease symptoms included wilt, chlorosis, and necrosis. Root length and colonization of the roots by the mycorrhizal fungi were determined by a modification of the gridline intersect method described by Giovannetti and Mosse (1980). Each root system was washed free of soil, blotted dry, arranged with roots in parallel alignment, and sectioned transversely at 2.5-cm-intervals. Random segments were withdrawn from each interval until a total of 0.5 g fresh weight of roots had been collected. These roots were cleared in 10% (w/v) potassium hydroxide, stained in 0.05% trypan blue in lactophenol (Phillips and Hayman, 1970), and evaluated for colonization by the mycorrhizal fungi.

The number of infection sites by the wilt fungus per 10 cm of root was evaluated by plating roots on a selective medium. Five 2.5-cm root segments per plant (taken from the sectioned root intervals prepared for the evaluation of mycorrhizal fungus colonization) were surface-disinfected in 0.263% sodium hypochlorite for 2 min, rinsed in sterile deionized

water, and plated on modified peptone-penta-chloro-nitro-benzene (PCNB) agar (Nash and Snyder, 1962; Papavizas, 1967) minus oxgall. Plates were incubated for 4-7 days at 25 C in the dark, and the number of colonies per 10 cm root sample was counted.

Shoot and root dry weight were determined after drying for 36 hr at 70 C. Root dry weight was determined after removal of 0.5 g root fresh weight sample (for the evaluation of mycorrhizal fungus colonization) from each root system. Total root length per plant (r_t) was estimated by the following equation:

$$r_t = r_s \times c \times w_t ,$$

where r_s = root length per 0.5 g fresh weight root sample, c = root dry weight constant ([root fresh weight g^{-1}] ÷ [root dry weight g^{-1}]), and w_t = total root dry weight (g) per plant.

Numbers of chlamydospores of the mycorrhizal fungi were assayed by collecting a 50-g soil sample from each of three pots per treatment, concentrating the spores in each sample using the methods described for inoculum preparation, and counting the spores using a dissecting microscope (20X). For the assay of soil populations of F. oxysporum, a 5-g soil sample for each of two pots per treatment was suspended in 0.1% water agar containing 250 mg/l of streptomycin sulfate, and each of the soil dilutions was plated on five plastic petri plates of the PCNB medium. Plates were incubated for 7-10 days at 25 C in the dark. Colonies of F. oxysporum were distinguishable microscopically (based on spore morphologies) and macroscopically from colonies of other Fusarium spp. present on the plates. Colonies of F. oxysporum had larger diameters and were less cottony in appearance compared with other Fusarium spp. Verifications of the identity and pathogenicity

of representative colonies of F. oxysporum taken from platings of both root and soil samples from each harvest were provided by the method of Sanchez and coworkers (1975).

Data from all experiments were analyzed statistically and apriori treatment contrasts were made using a protected Least Significant Difference (LSD) procedure (Steele and Torrie, 1960). Preliminary analyses revealed a lack of significant linear or quadratic regressions (data presented and discussed in the Results and Discussion sections, respectively, of Part 1 of this dissertation) of ID of each mycorrhizal fungus and all plant growth and fungus activity dependent variables monitored. Therefore data were analyzed by fungus treatment by averaging over inoculum levels. Additionally unequal variances were obtained between experimental performances and between harvest dates in an analysis of variance procedure. Thus data are presented by experimental performance and harvest date. Further details on statistical analysis of these data are presented in the Results section of Part 1 of this dissertation.

Results

Chlorosis and wilt were observed in plants that were inoculated dually with either G. mosseae or G. etunicatum and Fol by as early as 20 and 22 days, respectively, after exposure to the wilt fungus (Table 1). Development of wilt symptoms in plants inoculated with Fol alone was delayed 6-11 days compared with plants which were inoculated dually. The earlier onset of disease symptoms in dually inoculated plants occurred regardless of whether the plants were established by transplanting or direct seeding. The order of earliest development of disease symptoms by fungus treatment generally was G. mosseae plus Fol, G. etunicatum plus Fol, and Fol alone irrespective of PO_4 amendments. A similar ordering of treatments for disease severity was observed 5 wk after inoculating transplants with either mycorrhizal fungus species and/or with Fol (Fig. 1). Disease symptoms were expressed most in plants inoculated dually compared with plants inoculated with Fol alone.

Treatment effects on fungal and plant growth variables varied with experiment. Means of all variables for each fungus treatment are shown by experiment for ease of interpretation (Tables 2 and 3). Statistical tests were conducted to identify whether significant linear or quadratic relationships existed between ID of each mycorrhizal fungus and each dependent variable in the presence or absence of Fol (Tables 4 and 5). The lack of consistent significant linear or quadratic relationships (excluding those between initial and recovered chlamydospores and ID and root colonization of the mycorrhizal fungi) was interpreted to mean that data from each inoculum level:fungus combination could be averaged for each fungus treatment. Consequently other statistical analyses subsequently were conducted using these averages. Data were analyzed statistically

by experimental performance (first, repeat) and harvest date (6 and 8 wk after inoculating transplants or seeds) for the effect of both fungus treatment and plant age at the time of exposure to inoculum of Fol on plant growth, and on the development of mycorrhizae and Fol (Tables 6-25).

Development of mycorrhizae never proceeded further than initial sites of colonization by the fungi in the root epidermis and cortex. The total number of sites per root system (c_t) was estimated by counting the number of sites in a 0.5 g root fresh weight sample per root system (c_s) using the method described by Giovannetti and Mosse (1980), and by using the following equation:

$$c_t = c_s \times c \times w_t ,$$

where c = the root dry weight constant, and w_t = total root dry weight per plant. There were no consistent relationships between the amount of mycorrhizae (number of sites or %) and plant age at time of inoculation, harvest, or experimental performance (Tables 11 and 17). Densities of chlamydospores recovered overall were significantly greater ($P < 0.01$, 16 pairs, by Wilcoxon's Signed Rank Test [WSRT], Steele and Torrie, 1960) for G. mosseae compared with G. etunicatum.

Plant growth was improved by both mycorrhizal fungi a greater number of times in the repeat compared with the first performance of each experiment. Overall compared with noninoculated plants (with or without PO_4 amendments), inoculations with a mycorrhizal fungus resulted in significantly greater ($P < 0.0001$, 64 pairs, by WSRT) heights, shoot and root dry weights, or more extensive root systems in the repeat but not in the first experimental performances of both experiments (Tables 7-10). The growth of noninoculated plants never was significantly better than that of plants inoculated with a mycorrhizal fungus alone. In contrast plant growth overall was reduced significantly ($P < 0.05$, 64 pairs,

by WSRT) by G. etunicatum plus Fol and/or G. mosseae plus Fol compared with Fol or Fol plus PO_4 in the first performance of each experiment, and was increased significantly ($P < 0.0001$, 64 pairs, by WSRT) by the dual inoculation treatments over Fol or Fol plus PO_4 in the repeat performances (Tables 15-18). Generally plant growth was less in the repeat compared with the first experimental performance; however, a statistical analysis was not performed comparing performances as a result of unequal variances in a preliminary analysis of variance.

Phosphorus amendments were applied to balance expected nutrient differences in plants inoculated with Fol alone compared with plants inoculated dually. These amendments significantly reduced ($P < 0.05$, 8 pairs, by WSRT) DS in plants inoculated with Fol (Table 12). Similarly dual inoculations with either mycorrhizal fungus overall significantly decreased ($P < 0.01$, 16 pairs, by WSRT) DS compared with plants inoculated with Fol alone without PO_4 (Tables 13-17). Phosphorus amendments tended to decrease DS (not significant) in plants inoculated with Fol alone compared with plants inoculated dually.

The activity of Fusarium spp. in soil varied with inoculations with each mycorrhizal fungus. Soil populations of Fusarium spp. were reduced significantly ($P < 0.05$, 16 pairs, by WSRT) when plants were inoculated dually with G. etunicatum and Fol compared with inoculating with Fol alone with or without PO_4, respectively (Tables 13 and 14). Populations of Fusarium spp. did not differ significantly when plants were inoculated dually with G. mosseae and Fol compared with inoculating with Fol alone with or without PO_4, respectively (Tables 15 and 16). Consistent relationships were not found between the ranking of fungus treatments and either the vertical spread of Fol in shoots or the number of infection

sites of Fol in roots. An inoculum level of 500 cpg of the wilt fungus resulted in severe disease by 6 wk after inoculation (Tables 12-17). By 8 wk after inoculation, plants in certain treatments had DS index values of 4.0.

Plant growth was affected differently by each mycorrhizal fungus when plants were inoculated dually with a mycorrhizal fungus and Fol. Plants inoculated with G. etunicatum and Fol overall were significantly taller, weighed more, and had more extensive root systems ($P < 0.01$, 32 pairs, by WSRT) compared with plants inoculated with G. mosseae and Fol (Table 17). Thus poorer plant growth was associated with G. mosseae and Fol compared with G. etunicatum and Fol.

The development of mycorrhizae was influenced by the length of time roots were exposed to the inoculum of each mycorrhizal fungus. The development of mycorrhizae (%) was less (not significant) 6 wk after inoculation in plants inoculated before and at transplanting (transplant experiment) compared with plants inoculated only at seeding time (seed experiment) (Tables 20-21 and 24-25). Similarly root length, root weight, and number of sites of root colonization by a mycorrhizal fungus were significantly greater ($P < 0.0001$, 24 pairs, by WSRT) in the transplanted compared with seeded plants 6 wk after inoculation. In that the number of root colonization sites and root length were estimated as functions of root weight, it is possible that larger root systems in the transplanted plants essentially diluted the percent of root colonization, while the actual number of sites of colonization on roots was greater in transplanted compared with seeded plants. By the 8 wk harvest date, both root colonization (%) and the number of colonization sites became more variable with respect to transplanted or seeded plants.

Plant age at the time of exposure to inoculum of Fol influenced disease development and the activity of Fusarium spp. in the soil. Disease severity, root infection sites, vertical spread of Fol up shoot, and Fusarium spp. soil populations overall were significantly greater ($P < 0.0001$, 59 pairs, by WSRT) in transplanted compared with seeded plants (Tables 22-25). Generally increased disease was associated with transplanted plants which had been inoculated with Fol and a mycorrhizal fungus and higher levels of development of mycorrhizae.

Contamination by Fusarium spp. occurred in soil and/or plants in almost every fungus treatment x experimental performance x harvest date combination, especially by the 8 wk harvest date. Spread of Fol appeared to be random in soil not infested specifically with the wilt fungus (Tables 6 and 12). Representative colonies from plants and soil from each inoculated and noninoculated treatment were evaluated in a seedling bioassay (Sanchez et al., 1975) to determine the percentage of colonies identidied positively as Fol. More than 80% of the isolates tested were identified as the wilt fungus. This percentage is similar to the background of F. oxysporum (nonpathogenic) propagules Guy and Baker (1977) found in a study on Fusarium wilt of pea. Both soil populations and the development of mycorrhizae in plants where contamination occurred were low relative to the IDs of each fungus established initially.

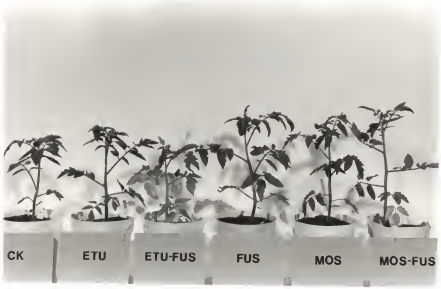

Fig. 1. Disease expression of Fusarium wilt of tomato cv. Manapal 5 wk after inoculation with Glomus etunicatum (ETU), G. mosseae (MOS), and/or with Fusarium oxysporum f. sp. lycopersici race 2 (-FUS) or noninoculated (CK). Symptoms of chlorosis and epinasty generally were present with ETU-FUS and MOS-FUS but were erratic in distribution in plants with FUS alone.

Table 1. The number of days after planting tomato (cv. Manapal) in soil infested with Fusarium oxysporum f. sp. lycopersici race 2 (Fol) and either Glomus etunicatum (Ge) or G. mosseae (Gm) to first symtoms of wilt or chlorosis

Plant age at time of exposure to Fol	Experimental performance	Days to first symptoms[y]		
		Ge + Fol	Gm + Fol	Fol
Transplant	First	23[z]	22	33
Transplant	Repeat	24	20	30
Seed	First	22	20	31
Seed	Repeat	22	22	32

[y]Earliest time symptoms first observed; symptoms were recorded without respect to either the initial inoculum level of each mycorrhizal fungus or to the addition of phosphorus to plants grown in soil infested with Fol alone.

[z]Based on thirty (Ge + Fol or Gm + Fol) or twenty (Fol with or without phosphorus amendments) replicates.

Table 2. Effect of planting tomato (cv. Manapal) transplants in soil infested with chlamydospores (0.1, 0.5, and 1.0 chlamydospore per g of soil [cpg]) of either Glomus etunicatum (Ge) or G. mosseae (Gm) and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) (500 cpg) on plant growth and on establishment and spread of the fungi

Treatment	Shoot growth				Root growth			
	height(cm)		dry weight(g)		dry weight(g)		root length(m)[o]	
	I[x]	II	I	II	I	II	I	II
6 wk after inoculation								
Noninoculated	34.6[z]	11.5	3.20	0.46	1.44	0.38	210	45
Noninoculated + PO_4[y]	40.4	10.8	3.36	0.32	1.26	0.22	166	27
Ge - 0.1	32.3	14.3	2.38	0.68	1.30	0.34	202	64
Ge - 0.5	47.0	16.0	3.44	0.56	1.58	0.40	193	90
Ge - 1.0	42.9	15.1	3.26	0.62	1.70	0.38	240	73
Gm - 0.1	45.3	13.8	3.22	0.44	1.36	0.34	183	66
Gm - 0.5	41.2	19.2	2.92	0.80	1.32	0.52	177	105
Gm - 1.0	37.6	15.4	2.70	0.70	1.34	0.53	169	132
Ge - 0.1 + Fol	28.4	12.2	2.30	0.58	1.23	0.38	138	53
Ge - 0.5 + Fol	20.3	11.6	1.14	0.43	0.74	0.20	82	59
Ge - 1.0 + Fol	24.4	13.1	1.30	0.48	0.98	0.26	111	50
Gm - 0.1 + Fol	28.4	13.0	1.90	0.34	1.30	0.12	138	32
Gm - 0.5 + Fol	28.1	10.7	1.26	0.50	1.00	0.40	109	89
Gm - 1.0 + Fol	34.1	11.2	1.60	0.50	1.42	0.40	148	86
Fol	33.8	11.3	2.08	0.63	1.30	0.45	122	88
Fol + PO_4	38.0	10.1	2.98	0.46	1.62	0.16	179	30
8 wk after inoculation								
Noninoculated	54.0	22.0	3.42	1.70	2.00	0.68	360	70
Noninoculated + PO_4	61.1	22.6	4.38	1.82	2.40	0.64	369	77
Ge - 0.1	47.9	25.2	3.62	1.68	1.78	0.78	371	91
Ge - 0.5	50.0	26.7	3.28	1.88	2.10	0.68	371	76
Ge - 1.0	65.9	23.8	3.84	1.70	2.06	0.68	351	83
Gm - 0.1	50.2	24.7	3.20	1.84	1.98	0.78	289	86
Gm - 0.5	59.4	27.1	3.48	2.00	1.60	1.04	275	122
Gm - 1.0	61.0	22.1	3.52,	1.72	1.58	0.66	323	69
Ge - 0.1 + Fol	35.2	18.0	1.98	0.78	0.96	0.50	174	61
Ge - 0.5 + Fol	33.2	20.7	1.70	1.26	0.80	0.58	174	83
Ge - 1.0 + Fol	35.3	16.8	1.64	1.25	0.70	0.34	189	45
Gm - 0.1 + Fol	38.9	22.0	2.14	0.95	0.70	0.50	173	68
Gm - 0.5 + Fol	29.2	16.8	1.56	0.50	0.80	0.33	155	33
Gm - 1.0 + Fol	34.2	14.3	1.66	0.60	0.58	0.33	116	37
Fol	31.8	16.5	0.97	0.40	0.46	0.75	61	82
Fol + PO_4	37.5	17.0	2.20	0.63	1.12	0.50	283	45

[o]Calculated by root length(m)/0.5 g root fresh weight x root dry weight constant x total root dry weight(g).

[p]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[q]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[r]Each value based on three replicates.

[s]Disease severity (D.S.) based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[t,u,v]Vertical spread (cm) or Fol up shoot (vert. spread), no. of Fol infection sites/10 cm root (I.S.), and population density of Fol (Log_{10} (colony forming units [c.f.u.]/g soil + 1)) evaluated on a selective medium.

[w]Each value based on two replicates.

[x]First (I) and repeat (II) experimental performances.

[y]Phosphorus (PO_4) amendments.

[z]Each value based on five replicates, unless noted otherwise.

Table 2--extended.

Mycorrhizae						Fol							
%P		no. sites/plant[q]		cpg[r]		D.S.[s]		vert. spread(cm)[t]		I.S.[u]		Log10(c.f.u./g+1)[v,w]	
I	II	I	II	I	II	I	II	I	II	I	II	I	II
0.00	0.00	0	0	0.01	0.00	0.0	0.0	0.0	0.0	1.4	1.0	0.00	1.13
0.06	0.00	11	0	0.00	0.00	0.0	0.0	0.0	2.0	2.8	1.7	2.58	3.14
0.75	0.55	143	37	0.01	0.02	0.0	0.0	4.0	0.0	0.0	1.3	0.00	3.22
0.72	0.09	145	8	0.05	0.11	0.0	0.0	2.0	0.0	1.4	4.3	0.00	3.35
1.45	0.00	386	0	0.13	0.15	0.0	0.0	4.0	0.0	1.4	2.0	0.00	2.62
0.07	0.13	14	6	0.04	0.01	0.0	0.0	2.0	0.0	2.0	6.7	2.48	3.18
0.24	0.55	47	44	0.19	0.14	0.0	0.0	0.0	4.0	0.4	5.7	2.89	3.09
0.67	0.61	116	28	0.32	0.27	0.0	0.0	0.0	0.0	3.2	3.0	2.90	3.09
2.42	0.61	290	26	0.01	0.01	1.5	2.2	22.5	9.8	5.5	6.0	0.00	3.69
4.38	0.42	335	30	0.04	0.09	2.8	2.5	13.8	10.0	6.6	7.7	2.52	3.87
1.25	0.23	129	10	0.05	0.09	3.2	1.6	18.0	10.0	8.0	9.3	1.21	3.64
1.00	0.29	89	6	0.21	0.02	2.6	3.2	22.6	10.0	5.4	10.3	2.82	3.67
1.69	0.33	111	13	0.22	0.10	3.0	2.6	20.0	9.0	7.6	10.3	3.18	3.88
0.53	1.53	70	158	0.39	0.35	2.6	3.0	24.8	9.0	6.5	7.3	3.21	3.78
0.22	0.13	20	13	0.00	0.00	2.6	2.3	30.0	9.8	6.4	8.0	2.55	3.73
0.19	0.00	32	0	0.00	0.00	2.2	2.6	30.0	9.2	7.6	11.3	2.59	3.55
0.00	0.00	0	0	0.00	0.01	0.0	0.0	24.0	0.0	6.0	2.0	0.96	2.73
0.37	0.00	0	0	0.05	0.00	0.0	0.0	50.0	0.0	14.3	1.3	1.01	2.22
0.98	0.34	368	30	0.00	0.03	0.0	0.0	40.0	0.0	18.8	7.0	1.68	3.28
2.58	0.49	793	41	0.03	0.07	0.0	0.0	34.0	0.0	14.2	4.3	1.77	2.60
3.32	0.32	1182	35	0.05	0.16	0.8	0.0	56.0	2.0	21.8	2.7	0.67	2.55
2.66	0.09	554	7	0.05	0.03	0.0	0.0	38.0	0.0	22.2	2.7	0.81	2.57
1.48	0.75	415	95	0.23	0.15	0.0	0.0	44.0	4.0	22.0	7.7	2.20	3.51
1.04	0.47	409	36	0.46	0.17	0.0	0.0	52.0	0.0	24.6	4.3	1.93	3.47
0.64	0.44	111	30	0.00	0.01	4.0	3.0	32.0	10.0	23.8	8.3	3.04	3.02
1.14	0.58	195	31	0.01	0.10	3.8	1.8	28.8	12.0	27.0	2.0	3.52	3.41
1.45	0.41	227	15	0.28	0.17	3.4	3.2	31.2	10.0	21.8	4.7	3.29	3.48
2.11	0.00	313	0	0.06	0.03	3.8	2.8	34.0	10.0	19.6	11.0	3.57	3.50
1.13	1.14	175	17	0.29	0.12	4.0	2.8	27.5	10.0	25.2	7.0	3.53	3.64
1.10	2.37	128	60	0.41	0.41	4.0	3.2	8.0	10.0	22.4	7.3	3.34	3.51
0.00	0.23	0	60	0.00	0.00	4.0	3.8	30.0	10.0	17.0	9.0	3.44	3.61
0.00	0.00	0	0	0.00	0.00	4.0	3.0	36.7	10.0	17.6	6.0	2.84	3.83

Table 3. Effect of planting tomato (cv. Manapal) seeds in soil infested with chlamydospores (0.1, 0.5, and 1.0 chlamydospore per g of soil [cpg]) of either Glomus etunicatum (Ge) or G. mosseae (Gm) and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) (500 cpg) on plant growth and on establishment and spread of the fungi

	Shoot growth				Root growth			
	height(cm)		dry weight(g)		dry weight(g)		root length(m)[n]	
Treatment	I[w]	II	I	II	I	II	I	II
6 wk after inoculation								
Noninoculated	32.0[y]	10.0	1.16	0.30	0.44	0.10	53	13
Noninoculated + PO_4[x]	36.9	9.5	1.00	0.10	0.28	0.02	41	5
Ge - 0.1	32.7	10.2	0.76	0.36	0.20	0.10	29	18
Ge - 0.5	31.7	9.1	0.88	0.26	0.46	0.10	66	15
Ge - 1.0	31.6	10.7	0.88	0.32	0.48	0.17	90	24
Gm - 0.1	35.0	10.9	0.90	0.35	0.54	0.13	97	18
Gm - 0.5	34.9	5.1	0.90	0.12	0.24	0.02	39	2
Gm - 1.0	40.2	9.5	1.56	0.26	0.42	0.10	65	17
Ge - 0.1 + Fol	33.4	12.3	0.94	0.33	0.52	0.15	112	33
Ge - 0.5 + Fol	30.4	5.0	0.76	0.20	0.30	0.02	55	4
Ge - 1.0 + Fol	33.2	10.3	0.84	0.40	0.36	0.15	50	22
Gm - 0.1 + Fol	16.2	9.0	0.36	0.23	0.22	0.03	14	12
Gm - 0.5 + Fol	24.5	7.8	0.83	0.23	0.64	0.02	86	4
Gm - 1.0 + Fol	27.6	4.0	0.83	0.07	0.35	0.25	35	39
Fol	33.6	6.5	0.80	0.13	0.58	0.02	76	3
Fol + PO_4	28.7	4.5	0.90	0.15	0.55	0.02	73	3
8 wk after inoculation								
Noninoculated	47.4	12.0	2.56	0.10	0.96	0.02	132	6
Noninoculated + PO_4	48.6	10.0	2.90	0.50	0.90	0.40	116	75
Ge - 0.1	40.0	24.0	2.76	1.48	0.96	0.78	134	176
Ge - 0.5	41.5	17.8	2.50	0.86	0.86	0.36	125	93
Ge - 1.0	41.7	19.3	2.68	1.18	0.98	0.58	160	136
Gm - 0.1	41.2	22.4	2.40	1.34	0.80	0.64	112	170
Gm - 0.5	43.7	15.5	3.26	0.80	0.74	0.54	120	116
Gm - 1.0	41.9	19.0	3.08	1.18	0.90	0.68	131	160
Ge - 0.1 + Fol	41.8	19.0	2.50	0.80	0.82	0.68	120	137
Ge - 0.5 + Fol	41.4	8.5	2.62	0.20	0.76	0.02	100	1
Ge - 1.0 + Fol	37.1	NC[z]	2.26	NC	0.84	NC	114	NC
Gm - 0.1 + Fol	25.3	7.7	1.50	0.20	0.53	0.03	48	11
Gm - 0.5 + Fol	33.7	13.0	4.06	0.80	0.64	0.40	98	107
Gm - 1.0 + Fol	27.1	12.0	2.13	0.60	0.60	0.30	98	85
Fol	27.8	7.5	1.74	0.10	0.76	0.02	116	5
Fol + PO_4	37.6	11.0	2.00	0.40	0.70	0.30	92	64

[n] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[o] Calculated by gridline intersect method (Giovannetti and Mosse, 1980).

[p] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[q] Each value based on three replicates.

[r] Disease severity (D.S.) based on a scale of 0-4; C = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[s,t,u] Vertical spread (cm) of Fol up shoot (vert. spread), no. of Fol infection sites/10 cm root (I.S.), and population density of Fol (Log_{10} (colony forming units [c.f.u.]/g soil + 1)) evaluated on a selective medium.

[v] Each value based on two replicates.

[w] First (I) and repeat (II) experimental performances.

[x] Phosphorus (PO_4) amendments.

[y] Each value based on five replicates, unless noted otherwise.

[z] Data not collected (NC).

Table 3--extended.

Mycorrhizae						Fol							
T^{o}		no. sites/plant[p]		cpg[q]		D.S.F		vert. spread(cm)[s]		I.S.[t]		$\log_{10}$(c.f.u./g+1)[u,v]	
I	II	I	II	I	II	I	II	I	II	I	II	I	II
0.00	0.00	0	0	0.00	0.01	0.0	2.0	0.0	7.5	NC	1.0	2.79	3.02
0.00	0.00	0	0	0.01	0.00	0.0	1.0	0.0	8.0	NC	3.4	2.97	3.49
2.34	0.31	52	8	0.03	0.01	0.2	0.6	0.0	7.4	NC	0.0	2.82	1.90
0.39	0.54	26	5	0.06	0.07	0.0	1.0	0.2	4.6	NC	0.0	2.55	1.96
0.73	3.31	56	12	0.17	0.07	0.0	1.0	0.0	8.8	NC	0.2	2.56	2.44
0.37	1.31	33	30	0.03	0.07	0.4	0.8	0.8	7.5	NC	0.5	2.32	0.81
1.09	1.95	45	5	0.10	0.07	0.0	0.2	2.0	1.8	NC	2.2	2.38	1.23
0.66	1.62	47	28	0.31	0.12	0.0	0.6	2.0	2.0	NC	NC	3.38	2.15
0.57	0.16	80	10	0.03	0.02	0.8	3.3	0.0	10.0	NC	1.8	2.50	3.04
1.56	0.48	39	1	0.10	0.06	1.2	3.0	2.0	5.0	NC	3.5	2.50	2.72
1.56	0.50	64	8	0.23	0.13	0.6	3.0	2.0	9.5	NC	1.0	2.80	2.46
3.33	0.10	57	2	0.04	0.03	1.8	2.0	2.0	8.7	NC	2.6	3.01	2.63
1.08	3.48	95	3	0.13	0.15	0.6	3.3	0.0	7.5	NC	0.8	2.59	3.16
0.95	0.20	37	3	0.28	0.38	2.3	3.3	0.0	3.5	NC	3.8	2.00	3.05
0.00	0.32	0	0	0.00	0.00	1.6	3.5	2.5	6.5	NC	3.6	2.69	3.40
0.00	0.51	0	1	0.00	0.00	1.0	3.0	0.0	4.5	NC	7.2	2.67	3.49
0.20	0.00	30	0	0.01	0.00	1.6	0.0	0.0	10.0	0.0	18.5	1.47	2.87
0.16	0.00	16	0	0.00	0.00	1.6	0.0	0.0	10.0	0.0	9.0	1.79	3.22
1.00	1.07	146	196	0.07	0.00	1.8	0.0	4.0	0.0	0.4	0.7	1.62	1.62
1.64	1.30	215	143	0.12	0.01	1.0	0.0	0.0	0.0	0.8	2.0	1.56	0.00
1.48	1.92	253	257	0.01	0.03	1.4	0.0	4.0	2.0	1.4	3.3	2.12	2.87
0.37	0.21	40	40	0.01	0.01	1.2	0.0	2.0	0.0	0.4	0.7	2.00	1.27
1.75	0.71	192	92	0.05	0.13	1.8	0.0	2.0	0.0	1.0	1.3	2.22	1.81
2.40	3.01	285	513	0.17	0.09	1.6	0.4	4.0	0.0	0.2	5.7	0.66	2.75
0.78	1.13	93	205	0.01	0.01	3.0	1.0	10.0	18.0	0.0	15.5	1.85	2.88
0.82	1.16	87	2	0.05	0.05	2.4	4.0	4.0	9.0	0.4	12.0	2.00	3.53
1.60	NC	188	NC	0.05	0.07	2.4	NC	0.0	NC	0.2	10.0	2.75	3.42
3.88	3.72	138	10	0.06	0.04	2.8	2.8	2.5	6.7	1.3	9.0	2.24	3.52
1.87	0.56	165	60	0.08	0.07	3.0	2.0	2.0	10.0	1.0	7.3	2.59	3.07
0.81	0.71	78	60	0.06	0.29	2.5	2.0	10.0	0.0	1.3	3.0	2.41	3.45
0.00	0.37	0	0	0.00	0.00	2.8	3.0	20.8	7.0	0.2	13.0	2.34	2.88
0.32	0.00	29	0	0.00	0.00	2.6	1.0	27.5	10.0	1.2	NC	2.37	3.38

Table 4. Linear or quadratic relationships of inoculum density (0.1, 0.5, and 1.0 chlamydospore per g of soil [cpg]) of Glomus etunicatum (Ge) or G. mosseae (Gm) in the presence or absence of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)(500 cpg) and tomato (cv. Manapal) growth or establishment and spread of the fungi, where transplants were planted in soil infested with a mycorrhizal fungus both prior to and simultaneously with Fol

	Shoot growth				Root growth			
	height(cm)		dry weight(g)		dry weight(g)		root length(m)[p]	
Treatment	I[y]	II	I	II	I	II	I	II
Linear - 6 wk after inoculation								
Ge	**[z]	NS	*	NS	*	NS	NS	NS
Gm	NS	NS	NS	*	NS	NS	NS	NS
Ge + Fol	NS	NS	*	NS	NS	NS	NS	NS
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Quadratic - 6 wk after inoculation								
Ge	NS	NS	NS	NS	NS	NS	NS	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Linear - 8 wk after inoculation								
Ge	**	NS	NS	NS	NS	NS	NS	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Quadratic - 8 wk after inoculation								
Ge	NS	NS	NS	NS	NS	NS	NS	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS

[p]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[q]Calculated by gridline intersect method (Giovannetti and Mosse, 1980).

[r]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Regressions based on nine data points.

[t]Disease severity (D.S.) based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[u,v,w]Vertical spread (cm) of Fol up shoot (vert. spread), no. of Fol infection sites/10 cm root (I.S.), and population density of Fol (Log_{10} (colony forming units [c.f.u.]/g soil + 1)) evaluated on a selective medium.

[x]Regressions based on six data points.

[y]First (I) and repeat (II) experimental performances.

[z]Probability (P) that linear or quadratic regression coefficients are significantly different ($P < 0.05$, *; < 0.01, **; not significant [NS]) from zero; regressions based on fifteen data points, unless noted otherwise.

Table 4--extended.

Mycorrhizae						Fol							
T[q]		no. sites/plant[r]		cpg[s]		D.S.[t]		vert.spread(cm)[u]		I.S.[v]		Log_{10}(c.f.u./g+1)[w,x]	
I	II	I	II	I	II	I	II	I	II	I	II	I	II
NS	NS	**	NS	**	**	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	**	**	NS	NS	NS	*	NS	NS	NS	NS
NS	NS	*	NS	NS	*	**	NS	NS	NS	NS	NS	*	NS
NS	NS	NS	**	**	**	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
**	NS	**	NS	NS	**	*	NS	NS	NS	NS	NS	NS	NS
*	NS	NS	NS	**	**	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	**	**	NS	NS	NS	NS	NS	NS	NS	NS
NS	**	NS	NS	**	**	NS	NS	*	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table 5. Linear or quadratic relationships of inoculum density (0.1, 0.5, and 1.0 chlamydospore per g of soil [cpg]) of Glomus etunicatum (Ge) or G. mosseae (Gm) in the presence of absence of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)(500 cpg) and tomato (cv. Manapal) growth or establishment and spread of the fungi, where seeds were planted in soil infested with a mycorrhizal fungus simultaneously with Fol

	Shoot growth				Root growth			
	height(cm)		dry weight(g)		dry weight(g)		root length(m)[p]	
Treatment	I[y]	II	I	II	I	II	I	II
Linear - 6 wk after inoculation								
Ge	NS*	NS	NS	NS	NS	NS	*	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NS	NS	NS	NS	NS	*	NS
Gm + Fol	*	NS	NS	NS	NS	NS	NS	NS
Quadratic - 6 wk after inoculation								
Ge	NS	NS	NS	NS	NS	NS	NS	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Linear - 8 wk after inoculation								
Ge	NS	NS	NS	NS	NS	NS	NS	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NC	NS	NC	NS	NC	NS	NC
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS
Quadratic - 8 wk after inoculation								
Ge	NS	NS	NS	NS	NS	NS	NS	NS
Gm	NS	NS	NS	NS	NS	NS	NS	NS
Ge + Fol	NS	NC	NS	NC	NS	NC	NS	NC
Gm + Fol	NS	NS	NS	NS	NS	NS	NS	NS

[p]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[q]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[r]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Regressions based on nine data points.

[t]Disease severity (D.S.) based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[u,v,w]Vertical spread (cm) of Fol up shoot (vert. spread), no. of Fol infection sites/10 cm root (I.S.), and population density of Fol (Log_{10} (colony forming units [c.f.u.]/g soil + 1)) evaluated on a selective medium.

[x]Regressions based on six data points.

[y]First (I) and repeat (II) experimental performances.

[z]Probability (P) that linear or quadratic regression coefficients are significantly different ($P < 0.05$, *; < 0.01, **; not significant [NS]) from zero; regressions based on fifteen data points, unless noted otherwise, or data not collected (NC).

Table 5--extended.

Mycorrhizae						Fol							
%[q]		no. sites/plant[r]		cpg[s]		D.S.[t]		vert. spread(cm)[u]		I.S.[v]		Log10(c.f.u./g+1)[w,x]	
I	II	I	II	I	II	I	II	I	II	I	II	I	II
*	**	NS	NS	**	NS	NS	NS	NS	NS	NC	NS	NS	NS
NS	NS	NS	NS	**	NS	NS	NS	NS	*	NC	NC	*	NS
NS	NS	NS	NS	**	**	NS	NS	NS	NS	NC	NS	NS	NS
**	NS	NS	NS	**	**	NS	NS	NS	*	NC	NS	*	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NC	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NC	NC	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NC	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NC	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
**	**	NS	**	**	NS	NS	NS	NS	NS	NS	NS	NS	*
NS	NC	NS	NC	NS	NS	NS	NC	NS	NC	NS	NS	NS	NS
**	*	NS	NS	NS	**	NS	NS	NS	*	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
NS	NC	NS	NC	NS	NS	NS	NC	NS	NC	NS	NS	NS	NS
NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS

Table 6. Effect of planting tomato (cv. Manapal) transplants or seeds in noninfested soil and weekly phosphorus (PO_4) amendments on plant growth and on contamination by and spread of mycorrhizal fungi and Fusarium oxysporum f. sp. lycopersici race 2 (Fol)

Parameter	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Noninoculated, Noninoculated + PO_4																
Plant growth																
Shoot height(cm)	34.6, 40.4	NS	54.0, 61.1	NS	32.0, 36.9	NS	47.4, 48.6	NS	11.5, 10.8	NS	22.0, 22.6	NS	10.0, 9.5	NS	12.0, 10.0	NS
Shoot dry weight(g)	3.20, 3.36	NS	3.42, 4.38	NS	1.16, 1.00	NS	2.56, 2.90	NS	0.46, 0.32	NS	1.70, 1.82	NS	0.30, 0.10	NS	0.10, 0.50	NS
Root dry weight(g)	1.44, 1.26	NS	2.00, 2.40	NS	0.44, 0.28	NS	0.96, 0.90	NS	0.38, 0.22	NS	0.68, 0.64	NS	0.10, 0.02	NS	0.02, 0.40	NS
Root length(m)[r]	210, 166	NS	360, 369	NS	53, 41	NS	132, 116	NS	45, 27	NS	70, 77	NS	13, 5	NS	6, 75	NS
Mycorrhizae																
Colonization(% root length)[s]	0.00, 0.06	NS	0.00, 0.30	NS	0.00, 0.00	NS	0.20, 0.16	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS
Colonization sites (no./plant)[t]	0, 11	NS	0,26	NS	0, 0	NS	30, 16	NS	0, 0	NS	0, 0	NS	0, 0	NS	0, 0	NS
Population density(chlamydospores/g dry soil)[u]	0.01, 0.00	NS	0.00, 0.05	NS	0.00, 0.01	NS	0.01, 0.00	NS	0.00, 0.00	NS	0.01, 0.00	NS	0.01, 0.00	NS	0.00, 0.00	NS
Fol																
Disease severity[v]	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	1.60, 1.60	NS	0.00, 0.00	NS	0.00, 0.00	NS	2.00, 1.00	*	0.00, 0.00	NS
Distance spread up shoot(cm)[w]	0.0, 0.0	NS	24.0, 50.0	**	0.0, 0.0	NS	0.0, 0.0	NS	0.0, 2.0	NS	0.0, 0.0	NS	7.5, 8.0	NS	10.0, 10.0	NS
Infection sites(no./10 cm root)[x]	1.4, 2.8	NS	6.0, 14.3	*	NC, NC	-	0.0, 0.0	NS	1.0, 1.7	NS	2.0, 1.3	NS	1.0, 3.4	NS	18.5, 9.0	**
Population density(Log_{10} (c.f.u./g + 1))[y,z]	0.00, 2.58	**	0.96, 1.01	NS	2.79, 2.97	NS	1.47, 1.79	NS	1.13, 3.14	**	2.73, 2.22	NS	3.02, 3.49	NS	2.87, 3.22	NS

[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five replicates, or data not collected (NC), unless noted otherwise.

[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u] Each value based on three replicates.

[v] Based on a scale on 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y] Based on plating stem or root tissue or soil on a selective medium.

[z] Colony forming units (c.f.u.); each value based on two replicates.

Table 7. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus etunicatum on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Noninoculated, G. etunicatum																
Plant growth																
Shoot height(cm)	34.6, 40.7	NS	54.0, 54.6	NS	32.0, 32.0	NS	47.4, 41.1	NS	11.5, 15.1	*	22.0, 25.5	NS	10.0, 10.0	NS	12.0, 20.4	NS
Shoot dry weight(g)	3.20, 3.03	NS	3.42, 3.58	NS	1.16, 0.84	NS	2.56, 2.65	NS	0.46, 0.62	NS	1.70, 1.75	NS	0.30, 0.31	NS	0.10, 1.17	NS
Root dry weight(g)	1.44, 1.53	NS	2.00, 1.98	NS	0.44, 0.38	NS	0.96, 0.93	NS	0.38, 0.37	NS	0.68, 0.71	NS	0.10, 0.13	NS	0.02, 0.57	*
Root length(m)[r]	210, 212	NS	360, 365	NS	53, 61	NS	132, 140	NS	45, 76	NS	70, 84	NS	13, 21	NS	6, 135	**
Mycorrhizae																
Colonization(% root length)[s]	0.00, 0.97	NS	0.00, 2.29	**	0.00, 1.18	NS	0.20, 1.37	*	0.00, 0.21	NS	0.00, 0.38	NS	0.00, 1.39	NS	0.00, 1.41	NS
Colonization sites (no./plant)[t]	0, 225	**	0, 781	**	0, 45	NS	30, 205	NS	0, 15	NS	0, 35	NS	0, 9	NS	0, 199	NS
Population density(chlamydospores g dry soil)[u]	0.01, 0.06	NS	0.00, 0.02	NS	0.00, 0.09	NS	0.01, 0.07	NS	0.00, 0.09	**	0.01, 0.09	**	0.01, 0.02	NS	0.00, 0.02	NS
Fol																
Disease severity[v]	0.00, 0.00	NS	0.00, 0.27	NS	0.00, 0.07	NS	1.60, 1.40	NS	0.00, 0.00	NS	0.00, 0.00	NS	2.00, 0.89	*	0.00, 0.00	NS
Distance spread up shoot(cm)[w]	0.0, 3.3	NS	24.0, 43.3	**	0.0, 0.7	NS	0.0, 2.7	NS	0.0, 0.0	NS	0.0, 0.7	NS	7.5, 6.9	NS	10.0, 0.7	**
Infection sites(no./10 cm root)[x]	1.4, 0.9	NS	6.0, 18.3	*	NC, NC	-	0.0, 0.9	NS	1.0, 2.7	NS	2.0, 4.7	NS	1.0, 0.2	NS	18.5, 2.0	**
Population density(Log_{10} (c.f.u./g + 1))[y,z]	0.00, 0.00	NS	0.96, 1.37	NS	2.79, 2.64	NS	1.47, 1.76	NS	1.13, 3.06	**	2.73, 2.81	NS	3.02, 2.10	NS	2.87, 1.50	**

[q]Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five (noninoculated) or fifteen (G. etunicatum) replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calulated by no. of individual sites of colonization/0.5g root fresh x root dry weight constant x total root dry weight(g).

[u]Each value based on three (noninoculated) or nine (G. etunicatum) replicates.

[v]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y]Based on plating stem or root tissue or soil on a selective medium.

[z]Colony forming units (c.f.u.); each value based on two (noninoculated) or six (G. etunicatum) replicates.

Table 8. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus etunicatum on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol), where noninoculated control plants received weekly phosphorus (PO_4) amendments

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Noninoculated + PO_4, G. etunicatum																
Plant growth																
Shoot height(cm)	40.4, 40.7	NS	61.1, 54.6	NS	36.9, 32.0	NS	48.6, 41.1	NS	10.8, 15.1	*	22.6, 25.2	NS	9.5, 10.0	NS	10.0, 20.4	*
Shoot dry weight(g)	3.36, 3.03	NS	4.38, 3.58	NS	1.00, 0.84	NS	2.90, 2.65	NS	0.32, 0.62	**	1.82, 1.75	NS	0.10, 0.31	NS	0.50, 1.17	NS
Root dry weight(g)	1.26, 1.53	NS	2.40, 1.98	NS	0.28, 0.38	NS	0.90, 0.93	NS	0.22, 0.37	NS	0.64, 0.71	NS	0.02, 0.13	NS	0.40, 0.57	NS
Root length(m)[r]	166, 212	*	369, 365	NS	41, 61	NS	116, 140	NS	27, 76	NS	77, 84	NS	5, 21	NS	75, 135	NS
Mycorrhizae																
Colonization(% root length)[s]	0.06, 0.97	NS	0.30, 2.29	**	0.00, 1.18	NS	0.16, 1.37	*	0.00, 0.21	NS	0.00, 0.38	NS	0.00, 1.39	NS	0.00, 1.43	NS
Colonization sites (no./plant)[t]	11, 225	**	26, 781	**	0, 45	NS	16, 205	NS	0, 15	NS	0, 35	NS	0, 9	NS	0, 199	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.06	NS	0.05, 0.02	NS	0.01, 0.09	NS	0.00, 0.07	NS	0.00, 0.09	**	0.00, 0.09	*	0.00, 0.02	NS	0.00, 0.02	NS
Fol																
Disease severity[v]	0.00, 0.00	NS	0.00, 0.27	NS	0.00, 0.07	NS	1.60, 1.40	NS	0.00, 0.00	NS	0.00, 0.00	NS	1.00, 0.89	NS	0.00, 0.00	NS
Distance spread up shoot(cm)[w]	0.0, 3.3	NS	50.0, 43.3	NS	0.0, 0.7	NS	0.0, 2.7	NS	2.0, 0.0	NS	0.0, 0.7	NS	8.0, 6.9	NS	10.0, 0.7	**
Infection sites(no./10 cm root)[x]	2.8, 0.9	NS	14.3, 18.3	NS	NC, NC	-	0.0, 0.9	NS	1.7, 2.7	NS	1.3, 4.7	NS	3.4, 0.2	NS	9.0, 2.0	**
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.58, 0.00	**	1.01, 1.37	NS	2.97, 2.64	NS	1.79, 1.76	NS	3.14, 3.06	NS	2.22, 2.81	NS	3.49, 2.10	**	3.22, 1.50	**

[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five (noninoculated + PO_4) or fifteen (G. etunicatum) replicates, or data not collected (NC), unless noted otherwise.

[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s] Calculated by a gridline intersect method (Giovannetti anf Mosse, 1980).

[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u] Each value based on three (noninoculated + PO_4) or nine (G. etunicatum) replicates.

[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y] Based on plating stem or root tissue or soil on a selective medium.

[z] Colony forming units (c.f.u.); each value based on two (noninoculated + PO_4) or six (G. etunicatum) replicates.

Table 9. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus mosseae on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Noninoculated, G. mosseae																
Plant growth																
Shoot height(cm)	34.6, 41.4	*	54.0, 56.9	NS	32.0, 36.7	NS	47.4, 42.3	NS	11.5, 16.1	**	22.0, 24.6	NS	10.0, 8.3	NS	12.0, 19.0	NS
Shoot dry weight(g)	3.20, 2.95	NS	3.42, 3.40	NS	1.16, 1.12	NS	2.56, 2.91	NS	0.46, 0.65	NS	1.70, 1.85	NS	0.30, 0.24	NS	0.10, 1.11	NS
Root dry weight(g)	1.44, 1.34	NS	2.00, 1.72	NS	0.44, 0.40	NS	0.96, 0.81	NS	0.38, 0.46	NS	0.68, 0.83	NS	0.10, 0.07	NS	0.02, 0.62	**
Root length(m)[r]	210, 176	NS	360, 296	NS	53, 67	NS	132, 121	NS	45, 99	NS	70, 92	NS	13, 18	NS	6, 149	**
Mycorrhizae																
Colonization(% root length)[s]	0.00, 0.33	NS	0.00, 1.73	**	0.00, 0.71	NS	0.20, 1.51	*	0.00, 0.42	NS	0.00, 0.44	NS	0.00, 1.65	NS	0.00, 1.31	NS
Colonization sites (no./plant)[t]	0, 59	NS	0, 459	**	0, 42	NS	30, 172	NS	0, 26	NS	0, 55	NS	0, 17	NS	0, 215	*
Population density(chlamydospores/g dry soil)[u]	0.01, 0.18	**	0.00, 0.25	**	0.00, 0.45	**	0.01, 0.08	NS	0.00, 0.14	**	0.01, 0.12	**	0.01, 0.09	*	0.00, 0.08	*
Fol																
Disease severity[v]	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.13	NS	1.60, 1.53	NS	0.00, 0.00	NS	0.00, 0.00	NS	2.00, 0.52	**	0.00, 0.13	NS
Distance spread up shoot(cm)[w]	0.0, 0.7	NS	24.0, 44.7	**	0.0, 4.0	NS	0.0, 2.0	NS	0.0, 2.7	NS	0.0, 1.3	NS	7.5, 3.5	NS	10.0, 0.0	**
Infection sites(no./10 cm root)[x]	1.4, 1.9	NS	6.0, 29.9	**	NC, NC	-	0.0, 0.5	NS	1.0, 5.1	*	2.0, 4.9	NS	1.0, 1.4	NS	18.5, 2.6	**
Population density(Log_{10} (c.f.u./g + 1))[y,z]	0.00, 2.76	**	0.96, 1.65	NS	2.79, 2.69	NS	1.48, 1.63	NS	1.13, 3.12	**	2.73, 3.18	NS	3.02, 1.39	**	2.87, 1.94	NS

[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five (noninoculated) or fifteen (G. mosseae) replicates, or data not collected (NC), unless noted otherwise.

[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u] Each value based on three (noninoculated) or nine (G. mosseae) replicates.

[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y] Based on plating stem or root tissue or soil on a selective medium.

[z] Colony forming units (c.f.u.); each value based on two (noninoculated) or six (G. mosseae) replicates.

Table 10. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus mosseae on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol), where noninoculated control plants received weekly phosphorus (PO_4) amendments

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Noninoculated + PO_4, G. mosseae																
Plant growth																
Shoot height(cm)	40.4, 41.4	NS	61.1, 56.9	NS	36.9, 36.7	NS	48.6, 42.3	NS	10.8, 16.1	**	22.6, 24.6	NS	9.5, 8.3	NS	10.0, 19.0	NS
Shoot dry weight(g)	3.36, 2.95	NS	4.38, 3.40	*	1.00, 1.12	NS	2.90, 2.91	NS	0.32, 0.65	**	1.82, 1.85	NS	0.10, 1.24	NS	0.50, 1.11	NS
Root dry weight(g)	1.26, 1.34	NS	2.40, 1.72	**	0.28, 0.40	NS	0.90, 0.81	NS	0.22, 0.46	NS	0.64, 0.83	NS	0.02, 0.07	NS	0.40, 0.62	NS
Root length(m)[r]	166, 176	NS	369, 296	NS	41, 67	NS	116, 121	NS	27, 99	*	77, 92	NS	5, 18	NS	75, 149	NS
Mycorrhizae																
Colonization(% root length)[s]	0.06, 0.33	NS	0.30, 1.73	*	0.00, 0.71	NS	0.16, 1.51	*	0.00, 0.42	NS	0.00, 0.44	NS	0.00, 1.65	NS	0.00, 1.31	NS
Colonization sites (no./plant)[t]	11, 59	NS	26, 459	**	0, 42	NS	16, 172	NS	0, 26	NS	0, 55	NS	0, 17	NS	0, 215	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.18	**	0.05, 0.25	**	0.01, 0.45	**	0.00, 0.08	NS	0.00, 0.14	**	0.00, 0.12	**	0.00, 0.09	*	0.00, 0.00	*
Fol																
Disease severity[v]	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.13	NS	1.60, 1.53	NS	0.00, 0.00	NS	0.00, 0.00	NS	1.00, 0.52	NS	0.00, 0.13	NS
Distance spread up shoot(cm)[w]	0.0, 0.7	NS	50.0, 44.7	NS	0.0, 4.0	NS	0.0, 2.0	NS	2.0, 2.7	NS	0.0, 1.3	NS	8.0, 3.5	*	10.0, 0.0	**
Infection sites(no./10 cm root)[x]	2.8, 1.9	NS	14.3, 29.9	**	NC, NC	-	0.0, 0.5	NS	1.7, 5.1	NS	1.3, 4.9	NS	3.4, 1.4	NS	9.0, 2.6	**
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.58, 2.76	NS	1.09, 1.65	NS	2.97, 2.69	NS	1.79, 1.63	NS	3.14, 3.12	NS	2.22, 3.18	NS	3.49, 1.39	**	3.22, 1.94	*

[q]Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five (noninoculated + PO_4) or fifteen (G. mosseae) replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on three (noninoculated + PO_4) or nine (G. mosseae) replicates.

[v]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y]Based on plating stem or root tissue or soil on a selective medium.

[z]Colony forming units (c.f.u.); each value based on two (noninoculated + PO_4) or six (G. mosseae) replicates.

Table 11. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of either Glomus etunicatum or G. mosseae on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
G. etunicatum, G. mosseae																
Plant growth																
Shoot height(cm)	40.7, 41.4	NS	54.6, 56.9	NS	32.0, 36.7	*	41.1, 42.3	NS	15.1, 16.1	NS	25.5, 24.6	NS	10.0, 8.3	NS	20.4, 19.0	NS
Shoot dry weight(g)	3.03, 2.95	NS	3.58, 3.40	NS	0.84, 1.12	NS	2.65, 2.91	NS	0.62, 0.65	NS	1.75, 1.85	NS	0.31, 0.24	NS	1.17, 1.11	NS
Root dry weight(g)	1.53, 1.34	NS	1.98, 1.72	NS	0.38, 0.40	NS	0.93, 0.81	NS	0.37, 0.46	NS	0.71, 0.83	NS	0.13, 0.07	NS	1.57, 0.62	NS
Root length(m)[r]	212, 176	*	365, 296	*	61, 67	NS	140, 121	NS	76, 99	NS	84, 92	NS	21, 18	NS	135, 149	NS
Mycorrhizae																
Colonization(% root length)[s]	0.97, 0.33	NS	2.29, 1.73	NS	1.18, 0.71	NS	1.37, 1.51	NS	0.21, 0.42	NS	0.38, 0.44	NS	1.39, 1.65	NS	1.43, 1.31	NS
Colonization sites (no./plant)[t]	225, 59	**	781, 459	**	45, 45	NS	205, 172	NS	15, 26	NS	35, 55	NS	9, 17	NS	199, 215	NS
Population density(chlamydospores/g dry soil)[u]	0.06, 0.18	**	0.02, 0.25	**	0.09, 0.45	**	0.07, 0.08	NS	0.09, 0.14	*	0.09, 0.12	NS	0.02, 0.09	**	0.02, 0.08	NS
Fol																
Disease severity[v]	0.00, 0.00	NS	0.27, 0.00	NS	0.07, 0.13	NS	1.40, 1.53	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.89, 0.52	NS	0.00, 0.13	NS
Distance spread up shoot(cm)[w]	3.3, 0.7	NS	43.3, 44.7	NS	0.7, 4.0	NS	2.7, 2.0	NS	0.0, 2.7	*	0.7, 1.3	NS	6.9, 3.5	**	0.7, 0.0	NS
Infection sites(no./10 cm root)[x]	0.9, 1.9	NS	18.3, 29.9	**	NC, NC	-	0.9, 0.5	NS	2.7, 5.1	NS	4.7, 4.9	NS	0.2, 1.4	NS	2.0, 2.6	NS
Population density(Log_{10} (c.f.u./g + 1))[y,z]	0.00, 2.76	**	1.37, 1.65	NS	2.64, 2.69	NS	1.76, 1.63	NS	3.06, 3.12	NS	2.81, 3.18	NS	2.10, 1.39	*	1.50, 1.94	NS

[q]Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on fifteen replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on nine replicates.

[v]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y]Based on plating stem or root tissue or soil on a selective medium.

[z]Colony forming units (c.f.u.); each value based on six replicates.

Table 12. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Fusarium oxysporum f. sp. lycopersici race 2 (Fol) and weekly phosphorus (PO_4) amendments on plant growth, establishment and spread of Fol, and on contamination by mycorrhizal fungi

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Fol, Fol + PO_4																
Plant growth																
Shoot height(cm)	33.8, 38.0	NS	31.8, 37.5	NS	33.6, 28.7	NS	27.8, 37.6	NS	11.3, 10.1	NS	16.5, 17.0	NS	6.5, 4.5	NS	7.5, 11.0	NS
Shoot dry weight(g)	2.08, 2.98	*	0.97, 2.20	*	0.80, 0.90	NS	1.74, 2.00	NS	0.63, 0.46	NS	0.40, 0.63	NS	0.13, 0.15	NS	0.10, 0.40	NS
Root dry weight(g)	1.30, 1.62	NS	0.46, 1.12	*	0.58, 0.55	NS	0.76, 0.70	NS	0.45, 0.16	NS	0.75, 0.50	NS	0.02, 0.02	NS	0.02, 0.30	NS
Root length(m)[r]	122, 179	NS	61, 283	**	76, 73	NS	116, 92	NS	88, 30	NS	82, 45	NS	3, 3	NS	5, 64	NS
Mycorrhizae																
Colonization(% root length)[s]	0.22, 0.19	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.12	NS	0.13, 0.00	NS	0.23, 0.00	NS	0.32, 0.51	NS	0.17, 0.00	NS
Colonization sites (no./plant)[t]	20, 32	NS	0, 0	NS	0, 0	NS	0, 29	NS	13, 0	NS	60, 0	NS	1, 1	NS	1, 0	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS
Fol																
Disease severity[v]	2.60, 2.20	NS	4.00, 4.00	NS	1.60, 1.00	NS	2.80, 2.60	NS	2.25, 2.60	NS	3.75, 3.00	NS	3.50, 3.00	NS	3.00, 1.00	NS
Distance spread up shoot(cm)[w]	30.0, 30.0	NS	30.0, 36.7	NS	2.5, 0.0	NS	20.8, 27.5	NS	9.8, 9.2	NS	10.0, 10.0	NS	6.5, 4.5	NS	7.0, 10.0	NS
Infection sites(no./10 cm root)[x]	6.4, 7.6	NS	17.0, 17.6	NS	NC, NC	-	0.2, 1.2	NS	8.0, 11.3	NS	9.0, 6.0	*	3.6, 7.2	*	13.0, NC	-
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.55, 2.59	NS	3.44, 2.84	NS	2.69, 2.67	NS	2.34, 2.37	NS	3.73, 3.55	NS	3.61, 3.83	NS	3.40, 3.49	NS	2.88, 3.38	NS

[q]Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on three replicates.

[v]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y]Based on plating stem or root tissue or soil on a selective medium.

[z]Colony forming units (c.f.u.); each value based on two replicates.

Table 13. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus etunicatum and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on plant growth and on establishment and spread of the fungi

Parameter	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Fol, G. etunicatum + Fol																
Plant growth																
Shoot height(cm)	33.8, 24.4	**	31.8, 34.6	NS	33.6, 32.3	NS	27.8, 40.1	**	11.3, 12.4	NS	16.5, 18.6	NS	6.5, 9.2	NS	7.5, 16.4	NS
Shoot dry weight(g)	2.08, 1.58	NS	0.97, 1.77	NS	0.80, 0.85	NS	1.74, 2.46	NS	0.63, 0.50	NS	0.40, 1.11	*	0.13, 0.33	NS	0.10, 0.68	NS
Root dry weight(g)	1.30, 0.98	NS	0.46, 0.82	NS	0.58, 0.39	NS	0.76, 0.81	NS	0.45, 0.28	NS	0.75, 0.47	NS	0.02, 0.09	NS	0.02, 0.17	NS
Root length(m)[r]	122, 111	NS	61, 179	**	76, 72	NS	116, 111	NS	88, 54	NS	82, 63	NS	3, 27	NS	5, 137	*
Mycorrhizae																
Colonization(% root length)[s]	0.22, 2.68	NS	0.00, 1.08	NS	0.00, 1.23	*	0.00, 1.07	NS	0.13, 0.41	NS	0.23, 0.48	NS	0.32, 0.39	NS	0.37, 1.14	NS
Colonization sites (no./plant)[t]	20, 251	**	0, 178	NS	0, 61	NS	0, 123	NS	13, 21	NS	60, 25	NS	1, 5	NS	1, 137	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.03	NS	0.00, 0.10	*	0.00, 0.12	**	0.00, 0.04	NS	0.00, 0.06	*	0.00, 0.09	*	0.00, 0.07	*	0.00, 0.04	NS
Fol																
Disease severity[v]	2.60, 2.57	NS	4.00, 3.73	NS	1.60, 0.87	*	2.80, 2.60	NS	2.25, 2.07	NS	3.75, 2.67	*	3.50, 3.14	NS	3.00, 2.50	NS
Distance spread up shoot(cm)[w]	30.0, 18.1	**	30.0, 30.7	NS	2.5, 1.3	NS	20.8, 4.7	**	9.8, 9.9	NS	10.0, 10.7	NS	6.5, 8.2	NS	7.0, 14.4	**
Infection sites(no./10 cm root)[x]	6.4, 6.7	NS	17.0, 24.2	*	NC, NC	-	0.2, 0.2	NS	8.0, 7.7	NS	9.0, 5.0	NS	3.6, 1.8	NS	13.0, 13.5	NS
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.55, 1.24	**	3.44, 3.28	NS	2.69, 2.60	NS	2.34, 2.20	NS	3.73, 3.73	NS	3.61, 3.30	NS	3.40, 2.74	NS	2.88, 3.28	NS

[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five (Fol) or fifteen (G. etunicatum + Fol) replicates, or data not collected (NC), unless noted otherwise.

[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u] Each value based on three (Fol) or nine (G. etunicatum + Fol) replicates.

[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y] Based on plating stem or root tissue or soil on a selective medium.

[z] Colony forming units (c.f.u.); each value based on two (Fol) or six (G. etunicatum + Fol) replicates.

Table 14. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus etunicatum and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on plant growth and on establishment and spread of the fungi, where plants grown in Fol-infested soil received weekly phosphorus (PO_4) amendments

Parameter	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Fol + PO_4, G. etunicatum + Fol																
Plant growth																
Shoot height(cm)	38.0, 24.4	**	37.5, 34.6	NS	28.7, 32.3	NS	37.6, 40.1	NS	10.1, 12.4	NS	17.0, 18.6	NS	4.5, 9.2	NS	11.0, 16.4	NS
Shoot dry weight(g)	2.98, 1.58	**	2.20, 1.77	NS	0.90, 0.85	NS	2.00, 2.46	NS	0.46, 0.50	NS	0.63, 1.11	NS	0.15, 0.33	NS	0.40, 0.68	NS
Root dry weight(g)	1.62, 0.98	**	1.12, 0.82	NS	0.55, 0.39	NS	0.70, 0.81	NS	0.16, 0.28	NS	0.50, 0.47	NS	0.02, 0.29	NS	0.30, 0.17	NS
Root length(m)[r]	179, 111	**	283, 179	*	73, 72	NS	92, 111	NS	30, 54	NS	45, 63	NS	3, 27	NS	64, 137	NS
Mycorrhizae																
Colonization(% root length)[s]	0.19, 2.68	**	0.00, 1.08	NS	0.00, 1.23	*	0.32, 1.07	NS	0.00, 0.41	NS	0.00, 0.48	NS	0.51, 0.39	NS	0.00, 1.14	NS
Colonization sites (no./plant)[t]	32, 251	**	0. 178	NS	0, 61	NS	29, 123	NS	0, 21	NS	0, 25	NS	1, 5	NS	0, 137	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.03	NS	0.00, 0.10	*	0.00, 0.12	**	0.00, 0.04	NS	0.00, 0.06	NS	0.00, 0.09	*	0.00, 0.07	*	0.00, 0.05	NS
Fol																
Disease severity[v]	2.20, 2.57	NS	4.00, 3.73	NS	1.00, 0.87	NS	2.60, 2.60	NS	2.60, 2.07	NS	3.00, 2.67	NS	3.00, 3.14	NS	1.00, 2.50	NS
Distance spread up shoot(cm)[w]	30.0, 18.1	**	36.7, 30.7	NS	0.0, 1.3	NS	27.5, 4.7	**	9.2, 9.9	NS	10.0, 10.7	NS	4.5, 8.2	NS	10.0, 14.4	NS
Infection sites(no./10 cm root)[x]	7.6, 6.7	NS	17.6, 24.2	*	NC, NC	-	1.2, 0.2	NS	11.3, 7.7	*	6.0, 5.0	NS	7.2, 1.8	**	NC, 13.5	-
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.59, 1.24	**	2.84, 3.28	NS	2.67, 2.60	NS	2.37, 2.20	NS	3.55, 3.73	NS	3.83, 3.30	NS	3.49, 2.74	NS	3.38, 3.28	NS

[q]Probability (P); P <0.05 (*); <0.01 (**); not significant (NS); each value based on five (Fol + PO_4) or fifteen (G. etunicatum + Fol) replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giocannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on three (Fol + PO_4) or nine (G. etunicatum + Fol) replicates.

W,X,[y]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[z]Based on plating stem or root tissue or soil on a selective medium.

[z]Colony forming units (c.f.u.); each value based on two (Fol + PO_4) or six (G. etunicatum + Fol) replicates.

Table 15. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus mosseae and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on plant growth and on establishment and spread of the fungi

Parameter	Time after planting (first performance)									Time after planting (repeat performance)							
	Transplants				Seeds					Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk			6 wk		8 wk		6 wk		8 wk	
	Means	P[q]	Means	P	Means	P	Means	P		Means	P	Means	P	Means	P	Means	P
Fol, G. mosseae + Fol																	
Plant growth																	
Shoot height(cm)	33.8, 30.2	NS	31.8, 34.1	NS	33.6, 22.8	**	27.8, 28.7	NS		11.3, 11.4	NS	16.5, 17.2	NS	6.5, 7.2	NS	7.5, 9.6	NS
Shoot dry weight(g)	2.08, 1.59	NS	0.97, 1.79	NS	0.80, 0.67	NS	1.74, 2.56	*		0.63, 0.45	NS	0.8, 0.66	NS	0.13, 0.18	NS	0.10, 0.37	NS
Root dry weight(g)	1.30, 1.24	NS	0.46, 0.69	NS	0.58, 0.40	NS	0.76, 0.59	NS		0.45, 0.31	NS	0.75, 0.38	NS	0.02, 0.08	NS	0.02, 0.16	NS
Root length(m)[r]	122, 132	NS	61, 148	*	76, 45	NS	116, 81	NS		88, 69	NS	82, 43	NS	3, 30	NS	5, 54	NS
Mycorrhizae																	
Colonization(% root length)[s]	0.22, 1.07	NS	0.00, 1.45	*	0.00, 1.79	**	0.00, 2.19	**		0.13, 0.72	NS	0.23, 1.35	NS	0.32, 1.15	NS	0.37, 2.18	NS
Colonization sites (no./plant)[t]	20, 90	NS	0, 205	NS	0, 63	NS	0, 127	NS		13, 59	*	60, 29	NS	1, 3	NS	1, 35	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.28	**	0.00, 0.25	**	0.00, 0.15	**	0.00, 0.07	NS		0.00, 0.16	**	0.00, 0.18	**	0.00, 0.21	**	0.00, 0.13	**
Fol																	
Disease severity[v]	2.60, 2.73	NS	4.00, 3.93	NS	1.60, 1.50	NS	2.80, 2.77	NS		2.25, 2.93	*	3.73, 2.93	NS	3.50, 2.87	NS	3.00, 2.50	NS
Distance spread up shoot(cm)[w]	30.0, 22.5	**	30.0, 22.9	NS	2.5, 0.7	NS	20.8, 4.6	**		9.8, 9.3	NS	10.0, 10.0	NS	6.5, 6.9	NS	7.0, 6.0	NS
Infection sites(no./10 cm root)[x]	6.4, 6.5	NS	17.0, 22.4	NS	NC, NC	-	0.2, 1.2	NS		8.0, 9.3	NS	9.0, 8.4	NS	3.6, 2.4	NS	13.0, 6.4	NS
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.55, 3.07	NS	3.44, 3.48	NS	2.69, 2.53	NS	2.34, 2.41	NS		3.73, 3.77	NS	3.61, 3.55	NS	3.40, 2.95	NS	2.88, 3.35	NS

[q]Probability (P); $P < 0.05$ (*); <0.01 (**); not significant (NS); each value based on five (Fol) or fifteen (G. mosseae + Fol) replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on three (Fol) or nine (G. mosseae + Fol) replicates.

[w,x,y]Based on a scale on 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[z]Colony forming units (c.f.u.); each value based on two (Fol) or six (G. mosseae + Fol) replicates.

Table 16. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of Glomus mosseae and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on plant growth and on establishment and spread of the fungi, where plants grown in Fol-infested soil received weekly phosphorus (PO_4) amendments

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[q]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
Fol + PO_4, G. mosseae + Fol																
Plant growth																
Shoot height(cm)	38.0, 30.2	*	37.5, 34.1	NS	28.7, 22.8	NS	37.6, 28.7	NS	10.1, 11.4	NS	17.0, 17.2	NS	4.5, 7.2	NS	11.0, 9.6	NS
Shoot dry weight(g)	2.98, 1.59	**	2.20, 1.79	NS	0.90, 0.67	NS	2.00, 2.56	NS	0.46, 0.45	NS	0.63, 0.66	NS	0.15, 0.18	NS	0.40, 0.37	NS
Root dry weight(g)	1.62, 1.24	*	1.12, 0.69	*	0.55, 0.40	NS	0.70, 0.59	NS	0.16, 0.31	NS	0.50, 0.38	NS	0.02, 0.08	NS	0.30, 0.16	NS
Root length(m)[r]	179, 132	*	283, 148	**	73, 45	NS	92, 81	NS	30, 69	NS	45, 43	NS	3, 30	NS	64, 54	NS
Mycorrhizae																
Colonization(% root length)[s]	0.19, 1.07	NS	0.00, 1.45	*	0.00, 1.79	**	0.32, 2.19	**	0.00, 0.72	NS	0.00, 1.35	*	0.51, 1.15	NS	0.00, 2.18	NS
Colonization sites (no./plant)[t]	32, 90	NS	0, 205	NS	0, 63	NS	29, 127	NS	0, 59	**	0, 29	NS	1, 3	NS	0, 35	NS
Population density(chlamydospores/g dry soil)[u]	0.00, 0.28	**	0.00, 0.25	**	0.00, 0.15	**	0.00, 0.07	NS	0.00, 0.16	**	0.00, 0.18	**	0.00, 0.21	**	0.00, 0.11	**
Fol																
Disease severity[v]	2.20, 2.73	NS	4.00, 3.93	NS	1.00, 1.50	NS	2.60, 2.77	NS	2.60, 2.93	NS	3.00, 2.93	NS	3.00, 2.87	NS	1.00, 2.50	NS
Distance spread up shoot(cm)[w]	30.0, 22.5	**	36.7, 22.9	*	0.0, 0.7	NS	27.5, 4.6	**	9.2, 9.3	NS	10.0, 10.0	NS	4.5, 6.9	NS	10.0, 6.0	NS
Infection sites(no./10 cm root)[x]	7.6, 6.5	NS	17.6, 22.4	NS	NC, NC	-	1.2, 1.2	NS	11.3, 9.3	NS	6.0, 8.4	NS	7.2, 2.4	**	NC, 6.4	-
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.59, 3.07	NS	2.84, 3.48	NS	2.67, 2.53	NS	2.37, 2.41	NS	3.55, 3.77	NS	3.83, 3.55	NS	3.49, 2.95	NS	3.38, 3.35	NS

[q]Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS); each value based on five (Fol + PO_4) or fifteen (G. mosseae + Fol) replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on three (Fol + PO_4) or nine (G. mosseae + Fol) replicates.

[w,x,y]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[z]Colony forming units (c.f.u.); each value based on two (Fol + PO_4) or six (G. mosseae + Fol) replicates.

Table 17. Effect of planting tomato (cv. Manapal) transplants or seeds in soil infested with chlamydospores of either Glomus etunicatum or G. mosseae and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on plant growth and on establishment and spread of the fungi

	Time after planting (first performance)								Time after planting (repeat performance)							
	Transplants				Seeds				Transplants				Seeds			
	6 wk		8 wk		6 wk		8 wk		6 wk		8 wk		6 wk		8 wk	
Parameter	Means	P[1]	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P	Means	P
G. etunicatum + Fol, G. mosseae + Fol																
Plant growth																
Shoot height(cm)	24.4, 30.2	*	34.6, 34.1	NS	32.3, 22.8	**	40.1, 28.7	**	12.4, 11.4	NS	18.6, 17.2	NS	9.2, 7.2	NS	16.4, 9.6	NS
Shoot dry weight(g)	1.58, 1.59	NS	1.77, 1.79	NS	0.85, 0.67	NS	2.46, 2.56	NS	0.50, 0.45	NS	1.11, 0.66	NS	0.33, 0.18	NS	0.68, 0.37	NS
Root dry weight(g)	0.98, 1.24	*	0.82, 0.69	NS	0.39, 0.40	NS	0.81, 0.59	NS	0.28, 0.31	NS	0.47, 0.38	NS	0.09, 0.08	NS	0.17, 0.16	NS
Root length(m)[r]	111, 132	NS	179, 148	NS	72, 45	NS	111, 81	NS	54, 69	NS	63, 43	NS	27, 30	NS	137, 54	NS
Mycorrhizae																
Colonization(% root length)[s]	2.68, 1.07	**	1.08, 1.45	NS	1.23, 1.79	NS	1.07, 2.19	**	0.41, 0.72	NS	0.48, 1.35	NS	0.39, 1.15	NS	1.14, 2.18	**
Colonization sites (no./plant)[t]	251, 90	**	178, 205	NS	61, 63	NS	123, 127	NS	21, 59	*	25, 29	NS	5, 3	NS	137, 35	NS
Population density(chlamydospores/g dry soil)[u]	0.03, 0.28	**	0.10, 0.25	**	0.12, 0.15	NS	0.04, 0.07	NS	0.06, 0.16	**	0.09, 0.18	**	0.07, 0.21	**	0.04, 0.13	**
Fol																
Disease severity[v]	2.57, 2.73	NS	3.73, 3.93	NS	0.87, 1.50	*	2.60, 2.77	NS	2.07, 2.93	**	2.67, 2.93	NS	3.14, 2.87	NS	2.50, 2.50	NS
Distance spread up shoot(cm)[w]	18.1, 22.5	*	30.7, 22.9	*	1.3, 0.7	NS	4.7, 4.6	NS	9.9, 9.3	NS	10.7, 10.0	NS	8.2, 6.9	NS	14.4, 6.0	**
Infection sites(no./10 cm root)[x]	6.7, 6.5	NS	24.2, 22.4	NS	NC, NC	-	0.2, 1.2	NS	7.7, 9.3	NS	5.0, 8.4	*	1.8, 2.4	NS	13.5, 6.4	**
Population density(Log_{10} (c.f.u./g + 1))[y,z]	1.24, 3.07	**	3.28, 3.48	NS	2.60, 2.53	NS	2.20, 2.41	NS	3.73, 3.77	NS	3.30, 3.55	NS	2.74, 2.95	NS	3.28, 3.35	NS

[1]Probability (P); P <0.05 (*); <0.01 (**); not significant (NS); each value based on fifteen replicates, or data not collected (NC), unless noted otherwise.

[r]Calculated by root length(m)/0.5g root ffesh weight x root dry weight constant x total root dry weight(g).

[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u]Each value based on nine replicates.

[v]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.

[w,x,y]Based on plating stem or root tissue or soil on a selective medium.

[z]Colony forming units (c.f.u.); each value based on six replicates.

Table 18. Influence of tomato (cv. Manapal) plant age at planting time (transplants, seeds) on plant growth and on contamination by and spread of mycorrhizal fungi and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) in noninoculated plants

Parameter	Time after planting (first)				Time after planting (repeat)			
	6 wk		8 wk		6 wk		8 wk	
	Means[p]	P[q]	Means	P	Means	P	Means	P
Noninoculated - transplants, seeds								
Plant growth								
Shoot height(cm)	34.6, 32.0	NS	54.0, 47.4	NS	11.5, 10.0	NS	22.0, 12.0	*
Shoot dry weight(g)	3.20, 1.16	**	3.42, 2.56	NS	0.46, 0.30	NS	1.70, 0.10	NS
Root dry weight(g)	1.44, 0.44	**	2.00, 0.96	**	0.38, 0.10	NS	0.68, 0.02	**
Root length(m)[r]	210, 53	**	360, 132	**	45, 13	NS	70, 6	NS
Mycorrhizae								
Colonization(% root length)[s]	0.00, 0.00	NS	0.00, 0.20	NS	0.00, 0.00	NS	0.00, 0.00	NS
Colonization sites (no./plant)[t]	0, 0	NS	0, 30	NS	0, 0	NS	0,0	NS
Population density(chlamydospores/g dry soil)[u]	0.01, 0.00	NS	0.00, 0.01	NS	0.00, 0.01	NS	0.01, 0.00	NS
Fol								
Disease severity[v]	0.00, 0.00	NS	0.00, 1.60	**	0.00, 2.00	**	0.00, 0.00	NS
Distance spread up shoot(cm)[w]	0.0, 0.0	NS	24.0, 0.0	**	0.0, 7.5	**	0.0, 10.0	**
Infection sites(no./10 cm root)[x]	1.4, NC	-	6.0, 0.0	NS	1.0, 1.0	NS	2.0, 18.5	**
Population density(Log_{10}(c.f.u./g + 1))[y,z]	0.00, 2.79	**	0.96, 1.47	NS	1.13, 3.02	**	2.73, 2.87	NS

[p] Each value based on five replicates (or data not collected [NC]), unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[u] Each value based on three replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[z] Colony forming units (c.f.u.); each value based on two replicates.

Table 19. Influence of tomato (cv. Manapal) plant age at planting time (transplant, seeds) and weekly phosphorus (PO_4) amendments on plant growth and on contamination by and spread of mycorrhizal fungi and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) in noninoculated plants

Parameter	Time after planting (first) 6 wk Means	P[q]	8 wk Means	P	Time after planting (repeat) 6 wk Means	P	8 wk Means	P
Noninoculated + PO_4 - transplants, seeds								
Plant growth								
Shoot height (cm)	40.4, 36.9	NS	61.1, 48.6	*	10.8, 9.5	NS	22.6, 10.0	*
Shoot dry weight (g)	3.36, 1.00	**	4.38, 2.90	**	0.32, 0.10	NS	1.82, 0.50	NS
Root dry weight (g)	1.26, 0.28	**	2.40, 0.90	**	0.22, 0.02	NS	0.64, 0.40	NS
Root length (m)[r]	166, 41	**	369, 116	**	27, 5	NS	77, 75	NS
Mycorrhizae								
Colonization (% root length)[s]	0.06, 0.00	NS	0.30, 0.16	NS	0.00, 0.00	NS	0.00, 0.00	NS
Colonization sites (no./plant)[t]	11, 0	NS	26, 16	NS	0,0	NS	0,0	NS
Population density (chlamydospores/g dry soil)[u]	0.00, 0.01	NS	0.05, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS
Fol								
Disease severity[v]	0.00, 0.00	NS	0.00, 1.60	**	0.00, 1.00	*	0.00, 0.00	NS
Distance spread up shoot (cm)[w]	0.0, 0.0	NS	50.0, 0.0	**	2.0, 8.0	**	0.0, 10.0	**
Infection sites (no./10 cm root)[x]	2.8, NC	-	14.3, 0.0	**	1.7, 3.4	NS	1.3, 9.0	**
Population density (Log_{10} (c.f.u./g + 1))[z]	2.58, 2.97	NS	1.01, 1.79	NS	3.14, 3.49	NS	2.22, 3.22	NS

[p] Each value based on five replicates (or data not collected [NC]), unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length (m)/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[u] Each value based on three replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[z] Colony forming units (c.f.u.); each value based on two replicates.

Table 20. Influence of tomato (cv. Manapal) plant age at time of exposure to inoculum of Glomus etunicatum (transplants, seeds) on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)

	Time after planting (first)				Time after planting (repeat)			
	6 wk		8 wk		6 wk		8 wk	
Parameter	Means[p]	P[q]	Means	P	Means	P	Means	P
G. etunicatum - transplants, seeds								
Plant growth								
Shoot height(cm)	40.7, 32.0	**	54.6, 41.1	**	15.1, 10.0	**	25.2, 20.4	**
Shoot dry weight(g)	3.03, 0.84	**	3.58, 2.65	**	0.62, 0.31	**	1.75, 1.17	*
Root dry weight(g)	1.53, 0.38	**	1.98, 0.93	**	0.37, 0.13	NS	0.71, 0.57	NS
Root length(m)[r]	212, 61	**	365, 140	**	76, 21	*	84, 135	**
Mycorrhizae								
Colonization(% root length)[s]	0.97, 1.18	NS	2.29, 1.37	*	0.21, 1.39	**	0.38, 1.43	**
Colonization sites (no./plant)[t]	225, 45	**	781, 205	**	15, 9	NS	35, 199	**
Population density(chlamydospores/g dry soil)[u]	0.06, 0.09	NS	0.02, 0.07	NS	0.09, 0.02	**	0.09, 0.02	**
Fol								
Disease severity[v]	0.00, 0.07	NS	0.27, 1.40	**	0.00, 0.89	**	0.00, 0.00	NS
Distance spread up shoot(cm)[w]	3.3, 0.7	NS	43.3, 2.7	**	0.0, 6.9	**	0.7, 0.7	NS
Infection sites(no./10 cm root)[x]	0.9, NC	-	18.3, 0.9	**	2.7, 0.2	*	4.7, 2.0	NS
Population density(Log_{10} (c.f.u./g + 1))[y,z]	0.00, 2.64	**	1.37, 1.76	NS	3.06, 2.10	**	2.81, 1.50	NS

[p] Each value based on fifteen replicates (or data not collected [NC]), unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[u] Each value based on nine replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[z] Colony forming units (c.f.u.); each value based on six replicates.

Table 21. Influence of tomato (cv. Manapal) plant age at time of exposure to inoculum of Glomus mosseae (transplants, seeds) on plant growth, development of mycorrhizae, and on contamination by and spread of Fusarium oxysporum f. sp. lycopersici race 2 (Fol)

Parameter	Time after planting (first) 6 wk Means[p]	P[q]	Time after planting (first) 8 wk Means	P	Time after planting (repeat) 6 wk Means	P	Time after planting (repeat) 8 wk Means	P
G. mosseae - transplants, seeds								
Plant growth								
Shoot height(cm)	41.4, 36.7	*	56.9, 42.3	**	16.1, 8.3	**	24.6, 19.0	**
Shoot dry weight(g)	2.94, 1.12	**	3.40, 2.91	NS	0.65, 0.24	**	1.85, 1.11	**
Root dry weight(g)	1.34, 0.40	**	1.72, 0.81	**	0.46, 0.07	**	0.83, 0.62	NS
Root length(m)[r]	176, 67	**	296, 121	**	99, 18	**	92, 149	**
Mycorrhizae								
Colonization(% root length)[s]	0.33, 0.71	NS	1.73, 1.51	NS	0.42, 1.65	**	0.44, 1.31	*
Colonization sites (no./plant)[t]	59, 42	NS	459, 172	**	26, 17	NS	55, 215	**
Population density(chlamydospores/g dry soil)[u]	0.18, 0.45	**	0.25, 0.08	**	0.14, 0.09	*	0.12, 0.08	NS
Fol								
Disease severity[v]	0.00, 0.13	NS	0.00, 1.53	**	0.00, 0.52	*	0.00, 0.13	NS
Distance spread up shoot(cm)[w]	0.7, 4.0	NS	44.7, 2.0	**	2.7, 3.5	NS	1.3, 0.0	NS
Infection sites(no./10 cm root)[x]	1.9, NC	-	29.9, 0.5	**	5.1, 1.4	**	4.9, 2.6	NS
Population density(Log_{10} (c.f.u./g + 1))[y,z]	2.76, 2.69	NS	1.65, 1.63	NS	3.12, 1.39	**	3.18, 1.94	**

[p] Each value based on fifteen replicates (or data not collected [NC], unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[u] Each value based on nine replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[z] Colony forming units (c.f.u.); each value based on six replicates.

Table 22. Influence of tomato (cv. Manapal) plant age at time of exposure to inoculum of Fusarium oxysporum f. sp. lycopersici race 2 (Fol) (transplants, seeds) on plant growth, establishment and spread of Fol, and on contamination by mycorrhizal fungi

Parameter	Time after planting (first) 6 wk Means[p]	P[q]	8 wk Means	P	Time after planting (repeat) 6 wk Means	P	8 wk Means	P
Fol - transplants, seeds								
Plant growth								
Shoot height (cm)	33.8, 33.6	NS	31.8, 27.8	NS	11.3, 6.5	NS	16.5, 7.5	NS
Shoot dry weight (g)	2.08, 0.80	**	0.97, 1.74	NS	0.63, 0.13	**	0.40, 0.10	NS
Root dry weight (g)	1.30, 0.58	**	0.46, 0.76	NS	0.45, 0.02	NS	0.75, 0.02	*
Root length (m)[r]	122, 76	NS	61, 116	NS	88, 3	NS	82, 5	NS
Mycorrhizae								
Colonization (% root length)[s]	0.22, 0.00	NS	0.00, 0.00	NS	0.13, 0.32	NS	0.23, 0.37	NS
Colonization sites (no./plant)[t]	20, 0	NS	0,0	NS	13, 1	NS	60, 1	NS
Population density (chlamydospores/g dry soil)[u]	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS
Fol								
Disease severity[v]	2.60, 1.60	*	4.00, 2.80	**	2.25, 3.50	**	3.75, 3.00	NS
Distance spread up shoot (cm)[w]	30.0, 4.0	**	30.0, 20.8	NS	9.8, 10.0	NS	7.5, 9.0	NS
Infection sites (no./10 cm root)[x]	6.4, NC	-	17.0, 0.2	*	8.0, 3.6	*	9.0, 13.0	NS
Population density (Log_{10} (c.f.u./g + 1)	2.55, 2.69	NS	3.44, 2.34	NS	3.73, 3.40	NS	3.61, 2.88	NS

[p] Each value based on five replicates (or data not collected [NC]), unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length (m)/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[u] Each value based on three replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[v] Colony forming units (c.f.u.); each value based on two replicates.

Table 23. Influence of tomato (cv. Manapal) plant age at time of exposure to inoculum of Fusarium oxysporum f. sp. lycopersici race 2 (Fol) (transplants, seeds) and weekly phosphorus (PO_4) amendments on plant growth, establishment and spread of Fol, and on contamination by mycorrhizal fungi

	Time after planting (first)				Time after planting (repeat)			
	6 wk		8 wk		6 wk		8 wk	
Parameter	Means[p]	P[q]	Means	P	Means	P	Means	P
Fol + PO_4 - transplants, seeds								
Plant growth								
Shoot height (cm)	38.0, 28.7	*	37.5, 37.6	NS	10.1, 4.5	*	17.0, 11.0	NS
Shoot dry weight (g)	2.98, 0.90	**	2.20, 2.00	NS	0.46, 0.15	NS	0.63, 0.40	NS
Root dry weight (g)	1.62, 0.55	**	1.12, 0.70	NS	0.16, 0.02	NS	0.50, 0.30	NS
Root length (m)[r]	179, 73	**	283, 92	**	30, 3	NS	45, 64	NS
Mycorrhizae								
Colonization (% root length)[s]	0.19, 0.00	NS	0.00, 0.32	NS	0.00, 0.51	NS	0.00, 0.00	NS
Colonization sites (no./plant)[t]	32, 0	NS	0, 29	NS	0, 1	NS	0, 0	NS
Population density (chlamydospores/g dry soil)[u]	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS	0.00, 0.00	NS
Fol								
Disease severity[v]	2.20, 1.00	**	4.00, 2.60	**	2.60, 3.00	NS	3.00, 1.00	NS
Distance spread up shoot (cm)[w]	30.0, 0.0	**	36.7, 24.0	NS	9.2, 9.7	NS	10.0, 10.0	NS
Infection sites (no./10 cm root)[x]	7.6, NC	-	17.6, 1.2	*	11.3, 7.2	*	6.0, NC	-
Population density (Log_{10} (c.f.u./g + 1))[y,z]	2.59, 2.67	NS	2.84, 2.37	NS	3.55, 3.49	NS	3.83, 3.38	NS

[p] Each value based on five replicates (or data not collected [NC]), unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length (m)/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[u] Each value based on three replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[z] Colony forming units (c.f.u.); each value based on two replicates.

Table 24. Influence of tomato (cv. Manapal) plant age at time of exposure to inoculum of Glomus etunicatum and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) (transplants, seeds) on plant growth and on establishment and spread of the fungi

Parameter	Time after planting (first) 6 wk Means[p]	P[q]	8 wk Means	P	Time after planting (repeat) 6 wk Means	P	8 wk Means	P
G. etunicatum + Fol - transplants, seeds								
Plant growth								
Shoot height (cm)	24.4, 32.3	**	34.6, 40.1	NS	12.4, 9.2	*	18.6, 16.4	NS
Shoot dry weight (g)	1.58, 0.85	**	1.77, 2.46	*	0.50, 0.33	NS	1.11, 0.68	NS
Root dry weight (g)	0.98, 0.39	**	0.82, 0.81	NS	0.28, 0.09	NS	0.47, 0.17	*
Root length (m)[r]	111, 72	*	179, 111	NS	54, 28	NS	63, 137	*
Mycorrhizae								
Colonization (% root length)[s]	2.68, 1.23	**	1.08, 1.07	NS	0.41, 0.39	NS	0.48, 1.14	NS
Colonization sites (no./plant)[t]	251, 61	**	178, 123	NS	21, 5	NS	25, 137	*
Population density (chlamydospores/g dry soil)[u]	0.03, 0.12	**	0.10, 0.04	NS	0.06, 0.07	NS	0.09, 0.04	NS
Fol								
Disease severity[v]	2.57, 0.87	**	3.73, 2.60	**	2.07, 3.14	**	2.67, 2.50	NS
Distance spread up shoot (cm)[w]	17.5, 1.3	**	30.7, 4.7	**	9.9, 8.6	NS	10.7, 11.7	NS
Infection sites (no./10 cm root)[x]	6.7, NC	-	24.2, 0.2	*	7.7, 1.8	**	5.0, 13.5	**
Population density (Log_{10} (c.f.u./g + 1))[y,z]	1.24, 2.60	**	3.28, 2.20	**	3.73, 2.74	**	3.30, 3.28	NS

[p] Each value based on fifteen replicates (or data not collected [NC]), unless noted otherwise.
[q] Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r] Calculated by root length (m)/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[s] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight (g).
[u] Each value based on nine replicates.
[v] Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y] Based on plating stem or root tissue or soil on a selective medium.
[z] Colony forming units (c.f.u.); each value based on six replicates.

Table 25. Influence of tomato (cv. Manapal) plant age at time of exposure to inoculum of Glomus mosseae and Fusarium oxysporum f. sp. lycopersici race 2 (Fol) (transplants, seeds) on plant growth and on establishment and spread of the fungi

Parameter	Time after planting (first) 6 wk Means[p]	P[q]	8 wk Means	P	Time after planting (repeat) 6 wk Means	P	8 wk Means	P
G. mosseae + Fol - transplants, seeds								
Plant growth								
Shoot height(cm)	30.2, 22.8	**	34.1, 28.7	NS	11.4, 7.2	**	17.2, 9.6	**
Shoot dry weight(g)	1.59, 0.67	**	1.79, 2.56	**	0.45, 0.18	**	0.66, 0.37	NS
Root dry weight(g)	1.24, 0.40	**	0.69, 0.59	NS	0.31, 0.08	NS	0.38, 0.16	NS
Root length(m)[r]	132, 45	**	148, 81	**	69, 30	NS	43, 54	NS
Mycorrhizae								
Colonization(% root length)[s]	1.07, 1.79	NS	1.45, 2.19	NS	0.72, 1.15	NS	1.35, 2.18	NS
Colonization sites (no./plant)[t]	90, 63	NS	205, 127	NS	59, 3	NS	29, 35	NS
Population density(chlamydospores/g dry soil)[u]	0.28, 0.15	**	0.25, 0.07	**	0.16, 0.21	*	0.18, 0.13	NS
Fol								
Disease severity[v]	2.73, 1.50	**	3.93, 2.77	**	2.93, 2.87	NS	2.93, 2.50	NS
Distance spread up shoot(cm)[w]	22.5, 0.7	**	22.9, 4.6	**	9.3, 6.9	NS	10.0, 6.0	**
Infection sites(no./10 cm root)[x]	6.5, NC	-	22.4, 1.2	*	9.3, 2.4	**	8.4, 6.4	NS
Population density(Log_{10} (c.f.u./g + 1))[y,z]	3.07, 2.53	*	3.48, 2.41	**	3.77, 2.95	*	3.55, 3.35	NS

[p]Each value based on fifteen replicates (or data not collected [NC]), unless noted otherwise.
[q]Probability (P); $P < 0.05$ (*); < 0.01 (**); not significant (NS).
[r]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[s]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[t]Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[u]Each value based on nine replicates.
[v]Based on a scale of 0-4; 0 = no symptoms and 4 = 100% of shoot exhibiting chlorosis, wilt, and/or necrosis.
[w,x,y]Based on plating stem or root tissue or soil on a selective medium.
[z]Colony forming units (c.f.u.); each value based on six replicates.

Discussion

Symptom expression of Fusarium wilt in plants inoculated with G. etunicatum and Fol or G. mosseae and Fol was advanced by as many as 11 days compared with plants inoculated with Fol alone. The order of initial symptom expression in inoculated plants generally was the same: first in G. mosseae and Fol (as early as 20 days after inoculation), next in G. etunicatum and Fol, and lastly in Fol alone.

Development of disease changed over time with respect to the mycorrhizal fungus treatments. During both experiments DS, both 6 and 8 wk after inoculation, was significantly less ($P < 0.01$, 16 pairs, by WSRT) in plants inoculated dually compared with plants inoculated with Fol alone. Adding PO_4 to plants inoculated with Fol appeared to reduce (not significant) DS compared with plants inoculated dually. Therefore while disease onset occurred first in plants inoculated dually, eventually (3-5 wk after disease onset) DS was reduced in plants inoculated dually compared with plants inoculated with Fol alone.

A PO_4 effect on plant growth was not observed in noninoculated plants or in plants inoculated with Fol alone. Consistent differences in each parameter evaluated were not found which could explain conclusively why both G. etunicatum and G. mosseae shortened the time to symptom onset but decreased DS compared with plants grown in soil infested with Fol alone. The PO_4 amendment appeared to reduce DS beyond the effect of the mycorrhizal fungi, so that a progression of increasing DS was found, where symptoms were least severe with Fol and PO_4, intermediate with either G. etunicatum or G. mosseae and Fol, and most severe with Fol alone.

Atypical root colonization by G. etunicatum and G. mosseae in this study may have had some bearing on the expression of Fusarium wilt symptoms

in plants inoculated dually with the wilt fungus. Root colonization by the mycorrhizal fungi was restricted to individual sites in which hyphae did not ramify inter- or intracellularly but remained as single-hypha entry points with a minimum number of surrounding cells invaded. This type of fungus-root development has been referred to by Smith and Bowen (1979) as the "soil phase", the initial stage of contact between the mycorrhizal fungus and the root. Developing entry points by each mycorrhizal fungus could have provided additional avenues for root invasion by Fol compared with other means by which Fol invades roots in the absence of mycorrhizal fungi. Early entrance into the roots by Fol could have resulted in earlier disease onset in plants inoculated dually compared with Fol alone, as was observed in both performances of both experiments.

In the absence of PO_4 amendments, DS 6 and 8 wk after inoculation may have been reduced by G. etunicatum and G. mosseae because growth of the mycorrhizal fungi in the roots became more extensive and their value to plant growth also became more pronounced. The PO_4 amendment resulted in greater (not significant) reduction in DS than did the mycorrhizal fungi. The phosphorus may have affected directly microbial changes pertinant to limiting the development of Fol (antagonism, competition), but more likely affected plant-mediated changes detrimental to further development of Fol.

In spite of restricted growth in the roots by the mycorrhizal fungi, improved growth occurred in plants inoculated with either mycorrhizal fungus compared with noninoculated plants. Shoot height, shoot and root dry weight, and total root length overall were increased significantly

($P < 0.0001$, 64 pairs, by WSRT) compared with noninoculated plants in the first performances but were not affected significantly in the repeat performances of each experiment. The means by which each fungus improved plant growth is not clear. Sanders and coworkers (1977) stressed the fact that low amounts of colonization by mycorrhizal fungi have a value to the host out of proportion to the fungal biomass involved. It is possible that the mycorrhizal fungi affected plant growth by influencing the nutrition or possibly hormonal levels in the plants.

The high native level of PO_4 (34.2-45.0 μg PO_4/g) in the soil used in this study probably eliminated the critical need for mycorrhizae (for improved uptake of P) by the plant. In fact high levels of PO_4 in roots can inhibit mycorrhizal colonization (Menge et al., 1978), but it is unknown whether the phosphate effects fungal growth within the root or limits development of extramatrical mycelia, thereby reducing secondary root colonization. In a different study (McGraw and Schenck, 1980), where soil PO_4 levels (69 μg PO_4/g) were as high as levels in the study described herein, tomato plants inoculated with G. etunicatum and G. mosseae had 31% and 39% root colonization, respectively, at 17 wk after inoculation. In contrast colonization did not occur in subsequent tests on several tomato cultivars using inoculum from these same isolates (N. C. Schenck, personal communication). Thus the low colonization observed in these experiments probably was not a result of high PO_4 levels in the soil.

Little attention has been given to the influence of PO_4 on Fusarium wilt of tomato. Walker and Foster (1946) found that plants grown in soil and fertilized with low-PO_4 solutions prior to inoculation were predisposed to more rapid wilt development compared with plants grown with

high PO_4 solutions. However, Jones and Woltz (1972) reported increased DS when high levels of superphosphate were applied to plants. In both cases nutrient imbalances, both internal and external to the roots, were suggested as factors influencing both the wilt fungus and the host: pathogen complex. Post inoculation experiments comparing the influence of low and high PO_4 levels on wilt are lacking.

Studies on plant-microbial interactions with mycorrhizal fungi generally have been conducted in low-PO_4 growth media or in field soils low in PO_4. To determine the role of PO_4 and mycorrhizae in influencing Fusarium wilt of tomato, it would be helpful to conduct similar experiments as described in this study in low-PO_4 soils.

Generally the two mycorrhizal fungi acted similarly in affecting changes in plant growth and altering the development of Fusarium wilt. However, differences did occur in relation to the magnitude of the affected changes by each mycorrhizal fungus. Glomus mosseae colonized (sites of colonization, %) roots more extensively (not significant) compared with G. etunicatum. The tendency toward greater levels of development with G. mosseae could help to explain why symptom expression occurred first and DS was greater (not significant) in plants inoculated dually with G. mosseae and Fol compared with plants inoculated dually with G. etunicatum and Fol. As was suggested previously, the entry points of G. mosseae could have allowed rapid establishment and development of Fol. Nyvall and Haglund (1972) found that DS was directly proportional to numbers of infection sites by F. oxysporum f. sp. pisi in Fusarium wilt of pea. Alternatively G. etunicatum may have limited DS by inducing resistance to the wilt fungus, relative to G. mosseae, by an unknown mechanism.

Although ID and distribution of the mycorrhizal fungi were considered in this study, consistent relationships were not detected between either ID and plant growth or ID and DS or activity of Fol in plant tissue or in soil. The population density in soil after 6 and 8 wk of both G. etunicatum and G. mosseae was the only parameter which consistently was related significantly ($P < 0.01$, 16 pairs, by WSRT) to initial ID. It is possible that if the experiments were repeated with more replicates and/or if more extensive root colonization by the mycorrhizal fungi had occurred significant relationships might be found between ID and plant growth, mycorrhizal fungus development, or DS.

Plant age (transplants, seeds) at the time of exposure to Fol influenced disease development but not disease onset. Establishing mycorrhizae in transplants prior to exposure to Fol did not alter the time of disease onset compared with plants inoculated simultaneously as seeds with a mycorrhizal fungus and Fol. However, the development of mycorrhizae, activity of Fol in plant tissue and in soil, and Fusarium wilt were affected by plant age. Disease severity, vertical spread of Fol up the shoot, root infection sites, and population density of Fusarium spp. in soil was significantly greater ($P < 0.0001$, 59 pairs, by WSRT) in transplanted compared with seeded plants. Similarly the number of root colonization sites by the mycorrhizal fungi, along with root length and root dry weight, was significantly greater ($P < 0.0001$, 24 pairs, by WSRT) in transplanted compared with seeded plants. It is possible that transplants are more susceptible to the wilt fungus, and perhaps to mycorrhizal fungi, compared with newly emerged seedlings possibly as a result of more entry (points) wounds created during transplantation.

The level of Fol used may have been excessive under the experimental

conditions employed. Disease occurred extensively in plants inoculated with Fol by 6 wk after inoculation and by 8 wk after inoculation, DS index values as high as 4.0 were reached in certain treatments. Guy and Baker (1977) found that a range of 287-1,080 propagules per gram of soil (15-35% of each level used were estimated to be background nonpathogenic F. oxysporum) of F. oxysporum f. sp. pisi resulted in DS levels of 50% on pea plants 8 wk after inoculation. A lower level of initial inoculum could have resulted in decreased symptom expression during the course of the experiments described herein. A more realistic test for the effect of mycorrhizae on Fusarium wilt may have been provided under such circumstances.

Results from a study by Dehne (1977) and Dehne and Schönbeck (1975) were similar to the results found in this study. Dehne and Schönbeck exposed nonmycorrhizal and mycorrhizal (G. mosseae) transplants (a German-bred cultivar, 'Rheinglut') of equivalent size to conidial inoculum (a propagule not considered to be the primary survival structure of Fusarium spp. according to Nash et al., 1961), and used sand as the growth medium. Reduced wilt was found in mycorrhizal compared with nonmycorrhizal plants which had been exposed to Fol. In spite of the vastly different biological systems used in this study compared with that by Dehne (1977) and Dehne and Schönbeck (1975), similar results were obtained. Further research is necessary to ascertain why PO_4 tended to result in lesser DS in plants inoculated with Fol alone compared with plants inoculated with a mycorrhizal fungus and Fol in the study described herein.

Characterization of experimental conditions which favor maximum mycorrhizae development has not been achieved. Colonization by mycorrhizal

fungi currently is known to be inhibited by excessive internal plant-phosphorus concentrations (Menge et al., 1978), incompatible host:mycorrhizal fungus combinations (Tinker, 1978), reduced light intensity (Furlan and Fortin, 1977), and soil temperature (Schenck and Schroeder, 1974). Similarly environmental factors can influence markedly the development of Fusarium wilt of tomato (Foster and Walker, 1947). The facilities in which these experiments were conducted were not designed to provide uniform ambient temperature, light intensity, and photoperiod and this may have contributed to many of the inconsistencies in the results. The use of growth chambers as an alternative environment for experimentation can impose practical limitations on the experimental design (size of plant growth containers, duration of plant growth, etc.). Clearly refining the biological system necessary to reflect natural conditions is difficult but probably essential to obtaining reliable data.

PART 2

THE INFLUENCE OF INOCULUM DENSITY OF GLOMUS ETUNICATUM AND G. MOSSEAE ON MYCORRHIZAL FUNGUS DEVELOPMENT AND ON TOMATO (CULTIVAR MANAPAL) GROWTH

Introduction

There have been numerous investigations of the relationships of both disease incidence and disease severity as functions of inoculum density (ID) for several soilborne fungal plant pathogens (Baker, 1971; Vanderplank, 1975). However, the relationship of ID of vesicular-arbuscular (VA) mycorrhizal fungi to root penetration and colonization and to host growth has been the subject of only a few investigations (Abbott and Robson, 1981; Carling et al., 1979; Daft and Nicolson, 1969, 1972; Daniels and McCool, 1981; Porter, 1979; Powell, 1981; Sanders et al., 1977; Smith and Walker, 1981). Rationales for selecting ID for use in mycorrhizae research have been independent of known ID relationships to fungus and host growth. Generally levels of ID used have a) not been quantified, i.e., a small amount of colonized root fragments with or without mycorrhizal fungus spore-infested soil was used (Abbott and Robson, 1978; Carling et al., 1979; Daft and Nicolson, 1969, 1972); b) not been quantified directly, i.e., ID was based on assays utilizing the "Most Probable Number" (MPN) method to estimate propagule densities (Porter, 1979; Powell, 1980; Smith and Walker, 1981); or c) have been low (i.e., ID of <0.01 propagule per gram of soil [ppg] was used) compared with a range (0.1-1.0 spore per gram of soil [spg]) of levels of

spore inoculum typically found in cultivated and noncultivated soils (Hayman and Stovold, 1979; Mosse and Bowen, 1968; Schenck and Kinloch, 1980).

Relationships have been found between increasing IDs and increasing plant and mycorrhizal fungus growth. Inoculum density of randomly distributed inoculum was related to the number of initial hyphal entry-points, and the number of entry-points was related to the length of colonized root tissue (Carling et al., 1979; Smith and Walker, 1981). Smith and Walker (1981) suggest "uniformly" distributed inoculum was used in their study, but their procedures indicate that the inoculum was distributed randomly. When low (< 0.05 propagule per gram of soil or 1 g of chopped mycorrhizal root segments per 150 g of soil) inoculum levels were used, linear relationships wete detected in root colonization as a function of ID (Carling et al., 1979; Smith and Walker, 1981). At high IDs, further increases in ID did not result in increased fungus development in the root system (Carling et al., 1979; Powell, 1981; Smith and Walker, 1981). Data reported by Powell (1981) can be interpreted to mean that initially ID was related linearly to shoot dry weight. Increases in white clover shoot dry weight occurred with increasing ID at 58 days after inoculation (where inoculum consisted of mixed species and propagule types), but not thereafter.

Comparisons between reports of actual IDs at which the relationship of ID:fungus growth changed from linear to curvilinear are not possible, in that researchers have based their propagule densities on estimates using the MPN method or using colonized root fragments. Additionally it would be difficult to ascertain what percentage of the fungus development could be attributed to a particular mycorrhizal fungus species when inoculum of mixed species was used (Powell, 1981; Smith and Walker, 1981). Daniels and McCool (1981) evaluated the influence of ID on root colonization

by six isolates of mycorrhizal fungi in sudangrass roots. At equivalent IDs, a single isolate of Glomus mosseae was assessed as having the greatest inoculum potential (effectiveness at colonizing roots on a per spore basis) while isolates G. fasciculatum-92, G. constrictum, G. fasciculatum-0-1, G. epigaeum, and G. fasciculatum-185 were 50, 50, 10.7, 7.2, and 4.1%, respectively, as effective as G. mosseae according to an MPN table. The influence of ID on host growth was not ascertained.

The effect of inoculum distribution, either aggregated, random, or uniform, has not been evaluated in mycorrhizae research. However, Smith and Walker (1981) concluded that uniform (random) inoculum distribution could influence levels of root colonization by mycorrhizal fungi compared with point-source inoculations. In general inoculum has been incorporated into the plant growth medium using either a point-source method (Abbott and Robson, 1981; Daft and Nicolson, 1969; Dehne, 1977; Dehne and Schönbeck, 1975; Porter, 1979), where inoculum is positioned at or below the predicted path of root growth or where a mycorrhizal plant is transplanted into noninfested soil, or by using a layering method. Smith and Walker (1981) attempted to obtain random inoculum distribution by mixing mycorrhizal fungus propagules contained in a nonsterile soil or mixed with treated sand such that the probability was high for the occurrence of uniform distances between spores in the three-dimensional volume. Using a point-source method of inoculation of tomato (Lycopersicon esculentum Mill. 'Eurocross'), Daft and Nicolson (1972) reported that an increase in spore numbers of Glomus macrocarpum of from 3 to 225 spores per plant resulted in linear relationships between the number of colonized root segments and the total number of root segments at 10 and 12 wk after inoculation. No relationship was found between

percent root colonization and plant dry weight, or between percent root colonization and inoculum density. Significant differences were not found between inoculated and noninoculated plants for plant weight, leaf length, or plant height until 10 wk after inoculation, and maximum root colonization by G. macrocarpum did not exceed 50% in their studies. Carling et al. (1979) speculated that at a harvest date preceding 12 wk, a relationship between ID and host growth might have occurred.

Differential growth of mycorrhizal compared with nonmycorrhizal plants may vary with the species or isolate of VA mycorrhizal fungus used (Abbott and Robson, 1977, 1978; Carling and Brown, 1980; McGraw and Schenck, 1980, 1981; Mosse, 1972a, 1972b). In addition, Mosse (1972b) reported that varying the soil type resulted in a permutation of the rankings of isolates of mycorrhizal fungi tested for their effects on host growth. Subfactors such as inoculum density or inoculum distribution were not considered for possible effects on the growth response of the host. The time of assessment of host growth response to different species of mycorrhizal fungi had a bearing on the ranking of species tested from the most to least effective at inducing a plant growth response. Thus a species x time interaction was observed (McGraw and Schenck, 1980). These observations of the influence of time on the effectiveness of the mycorrhizal fungi at inducing a plant growth response emphasize the need for serial monitoring during an experiment (McGraw and Schenck, 1980).

The objectives of this study were to evaluate relationships between ID of two species of mycorrhizal fungi to fungus and plant growth and development using randomly distributed inoculum and using propagule population densities in the range of values reported in the literature

for mycorrhizal fungi under field conditions. Understanding quantitative relationships between the growth and development of mycorrhizal fungi along with growth and development of the host could 1) help to determine whether mycorrhizal fungi have ID:fungus growth and ID:host growth relationships similar to those for several soilborne fungal plant pathogens; 2) aid in methodology of mycorrhizae research; and 3) provide improved opportunities for utilizing mycorrhizae to enhance crop productivity.

Materials and Methods

The isolates used in this study were: two isolates of G. etunicatum Becker & Gerd. (Ge-1, Ge-2), obtained from J. W. Gerdemann, University of Illinois and from R. Roncadori, University of Georgia, respectively; and two isolates of G. mosseae (Nicol. & Gerd.) Gerd. & Trappe (Gm-1, Gm-2), obtained from N. C. Schenck, University of Florida and B. Mosse, Rothamsted Experiment Station, England, respectively. Chlamydospores of each isolate were produced in pot cultures (Mosse, 1953) of bahiagrass (Paspalum notatum Flügge). The pot culture soil was dried to approximately 2% moisture content and was stored at 5 C until used. Chlamydospores from this stored pot culture soil were freed of other potential propagules, such as mycorrhizal root fragments, by decanting and wet-sieving (Gerdemann and Nicolson, 1963), and concentrated further by centrifuging at 1270 x g in water and 2 M sucrose for 3 and 1.5 min, respectively. Spore rinse-water, collected from each isolate after the last centrifugation, was mixed and then filtered three times through a 45-µm-mesh sieve.

The soil used was an autoclaved (121 C for two 4-hr periods on consecutive days) Lakeland fine sand that had a moderately high level of phosphorus (34.2-69.9 µg P/g), and had the following levels of other elements: 248-448 µg Ca/g; 0.36-0.92 µg Cu/g; 9.2-23.2 µg Fe/g; 32-104 µg K/g; 22.1-48.0 µg Mg/g; 18.0-22.3 µg Mn/g; 32.0 µg Zn/g; as well as a pH of 5.7-6.3 (analyzed by Soils Clinic, University of Florida).

Three experiments were conducted. Inoculum of each of the isolates was mixed randomly with the treated soil (according to the procedures described in Part 1 of this dissertation) to achieve initial inoculum levels of 0.0, 0.1, 1.0, and 10.0 chlamydospores per gram of soil (cpg)

in Experiment 1; 0.0, 0.1, 0.3, 0.5, 0.7, and 1.0 cpg in Experiment 2; and 0.0, 0.1, 0.5, and 1.0 cpg in Experiment 3. Spore rinse-water was mixed with noninfested soil (0.0 cpg) to ensure addition of a comparable microflora in noninfested compared with infested soil. Autoclaved infested soil was added at 600 g per 10.2-cm-diameter clay pot (Experiment 1) or 2000 g per 15.2-cm-diameter plastic pot (Experiments 2 and 3). The tomato cultivar Manapal was used in each experiment. In Experiment 1, three seeds (nondisinfected) per pot were planted in noninfested soil or in soil infested with isolates Ge-1, Ge-2, Gm-1, and Gm-2 (except that the 10.0-cpg level was omitted for Gm-2 because of insufficient spore numbers). Plants were thinned within 1 wk to one plant per pot. Experiment 2 was similar to Experiment 1, except that only two isolates (Ge-1 and Gm-1) were tested. In Experiment 3, plants of two ages were planted in infested or noninfested soil. For the first plant age (transplants), one seed was planted in autoclaved soil in 50-ml plastic beakers, where soil was infested with Ge-1 or Gm-1 at 0.1, 0.5, and 1.0 cpg or was noninfested (0.0 cpg). Two weeks after inoculation, the seedling and contents of each beaker were transplanted into a 15.2-cm-diameter plastic pot containing 2000 g of soil infested with either Ge-1 or Gm-1 at 0.1, 0.5, and 1.0 cpg. Seedlings established in noninfested soil were transplanted into noninfested soil. For the second plant age (seeds), seeds which were surface disinfected according to the procedures described in Part 1 of this dissertation were planted three per 15.2-cm-diameter plastic pot containing 2000 g of noninfested soil or soil infested with either Ge-1 or Gm-1 at 0.1, 0.5, and 1.0 cpg. Plants were thinned to one per pot within 1 wk. Experiment 3 was from Part 1 of this dissertation and was repeated.

All plants were maintained in a greenhouse where the temperatures ranged from 22-30 C. In all experiments, pots were randomized within but not between isolates. Plants were watered daily and fertilized weekly with 50 ml of 2X Hoagland's solution (Hoagland and Arnon, 1938) minus phosphorus.

For each experiment five plants per treatment (isolate x inoculum level combination) were harvested at each of the following sampling dates: in Experiment 1 at 2.5 and 5 wk after seedling emergence; in Experiment 2 at 2, 6, and 13 wk after seedling emergence; and in Experiment 3 at 6 and 8 wk after transplanting or seeding.

At each plant harvest date, the following data on plant growth were collected: plant height, shoot and root dry weight (dried for 36 hr at 70 C). Root dry weight was calculated after removal of samples for assessment of mycorrhizal fungus colonization. Additionally total root length per plant and root colonization by the mycorrhizal fungi were assessed according to the methods described in Part 1 of this dissertation. The total number of colonization sites per plant (where "site" refers to individual hypha that penetrated a root epidermal cell and only a few adjacent cortical cells) was calculated as in Part 1 of this dissertation. A colonization index (CI) was calculated when extensive areas of the cortex were invaded by the mycorrhizal fungus. The following equation was used to calculate the CI value:

$$CI = C_s \times W_t ,$$

where C_s = the number of root intersects colonized by the mycorrhizal fungus per 0.5 g root fresh weight sample, and W_t = the total root dry weight per plant. The CI was calculated to provide a relative comparison of percent root colonization values between treatments by adjusting

the values for differences in root dry weights. Data from each experiment were analyzed using standard regression methods, or by Duncan's multiple range test, Student's t-test, or by Wilcoxon's signed rank test (Steele and Torrie, 1960), where appropriate.

Linear regression was used to determine the presence of overall relationships between each variable and ID, and quadratic regression was used to determine whether relationships were linear or nonlinear. The multiple infection correction suggested by Gregory (1948) (Log_e 1/1-X, where X = proportion of root:gridline intersects colonized by the mycorrhizal fungus) was applied to the percent root colonization data prior to regression analysis.

Results

Means of tomato growth, mycorrhizal fungus root colonization, and population density as functions of ID are presented in Tables 26-28. Regression equations for those fungus species/isolate x date x variable combinations for which the regression was significant ($P < 0.05$) are presented in Tables 29-31.

Root colonization increased significantly ($P < 0.05$) with increasing ID of isolates Ge-1 and Gm-1 at 2.5 wk after seedling emergence and for isolates Ge-1 and Ge-2 at 5 wk after seedling emergence in Experiment 1 (Table 29), and for isolates Ge-1 and Gm-1 at 6 and 13 wk after seedling emergence in Experiment 2 (Table 30). In Experiment 3 at 6 wk after transplanting, root colonization increased with an increase in ID for Gm-1 in the first and repeat experimental performances and for Ge-1 in the repeat experimental performance (Table 31). Additional significant increases ($P < 0.05$) were detected in Experiment 3 for Gm-1 8 wk after seeding in both the first and repeat experimental performance, and for Ge-1 8 wk after transplanting in the first experimental performance.

Percent root colonization, the CI, and the number of colonization sites per plant increased significantly with an increase in ID in most cases. Where significant quadratic relationships were detected, several differences occurred between the CI and root colonization variables as functions of ID. Use of the CI variable resulted in a significant quadratic regression in Experiment 1 for Gm-1 at 5 wk after seedling emergence and in Experiment 2 for Ge-1 at 6 wk after seedling emergence. These relationships were not detected with the variable root colonization.

Increasing ID occasionally resulted in a less than proportionate increase in root colonization as detected by significant quadratic regressions. This apparent saturation effect was detected between ID and root colonization by the final harvest date in Experiments 1 and 2, and by the 6 wk harvest in Experiment 3 (Tables 29-31). The saturation effect was noted for Ge-1 at 5 wk after seedling emergence in Experiment 1 (Table 29), for Gm-1 at 13 wk after seedling emergence in Experiment 2 (Table 30), and for Gm-1 at 6 wk after seeding in the first but not in the repeat performance of Experiment 3 (Table 31).

Variation between experiments in levels of root colonization occurred. Colonization levels were greatest in Experiment 1 and least in Experiment 3. For example, the highest values assessed for Gm-1 were 50%, 19%, and 3% in Experiments 1, 2, and 3, respectively. The low (3%) value was a reflection of the restricted fungus growth in the root tissue in Experiment 3.

Relationships between ID and root colonization were influenced by the mycorrhizal fungus species tested. In Experiments 1 and 2, where levels were substantially more extensive than the individual sites of root colonization found in Experiment 3, root colonization by Gm-1 was significantly greater ($P < 0.01$, 21 pairs, by Wilcoxon's signed rank test) compared with Ge-1 for each inoculum level. In Experiment 3 where colonization was restricted to the initial "soil phase" of individual root colonization sites (Smith and Bowen, 1979), differences in root colonization (%) levels for isolates Gm-1 and Ge-1 were not significant. In Experiment 2 the increase in amount (%) of root colonization by Gm-1 became saturated with increasing ID at 13 wk but not at 6 wk after seedling emergence (Fig. 2). A saturation effect was not observed with Ge-1 at either the 6 or 13 wk date (Fig. 3). In Experiment 1 when

root colonization levels were higher, a significant regression equation was calculated for Ge-1 but not for Gm-1 (Table 29). Root colonization levels by any mycorrhizal fungus species tested never exceeded 50%.

Similar ID:root colonization relationships were detected for both isolates of each mycorrhizal fungus species. In Experiment 1 root colonization increased significantly in a linear relationship with increasing ID for Ge-1 and Ge-2 at both 2.5 and 5 wk after seedling emergence (Table 29). However, in Experiment 1 the rate of increase in root colonization as a function of ID was significantly greater ($P < 0.01$, by Student's t-test, 38 degrees of freedom [d.f.]) for Ge-2 compared with Ge-1 at 2.5 wk seedling emergence. Similarly root colonization by Gm-1 and Gm-2 at 2.5 wk but not at 5 wk after seedling emergence in Experiment 1 increased with an increase in ID from 0.1 to 1.0 cpg (Tables 26 and 29). Colonization by Gm-1 was significantly greater ($P < 0.05$, by Duncan's multiple range test) compared with Gm-2 at both dates at 1.0 but not 0.1 cpg (Fig. 4).

Relationships between ID and tomato growth were detected but were rare. Root dry weight (Experiment 2) or root length (Experiment 1, 2, and 3) were related curvilinearly to ID in several instances. Shoot height (Experiments 2 and 3) overall were affected less frequently than root growth by increasing IDs for both Ge-1 and Gm-1.

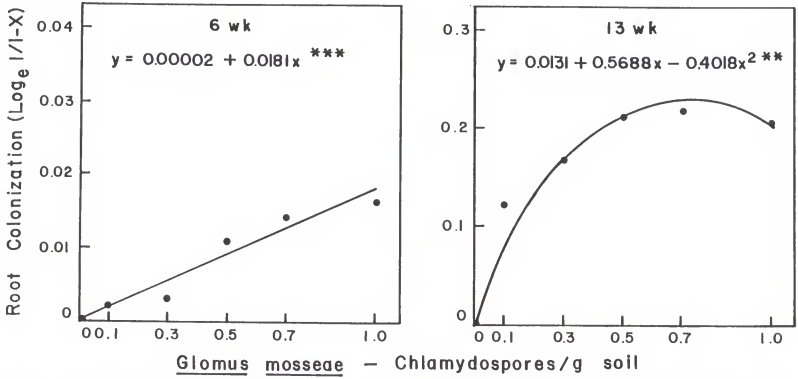

Fig. 2. The relationship of percentages of colonization of tomato (cv. Manapal) roots to initial densities of chlamydospores of G. mosseae (Florida isolate) 6 and 13 wk after seedling emergence, where seeds were planted in autoclaved infested soil. Prior to regression analysis, the data were transformed to Log_e 1/1-X, where X = proportion of intersects with mycorrhizal fungus root colonization as determined by a gridline intersect method described by Giovannetti and Mosse (1980). Equations calculated from 30 data points for each isolate x date combination are presented which possess a significant (***, **; $P < 0.001, < 0.01$) regression coefficient or coefficient of the squared term, respectively, for rejection of the null hypothesis that the regression coefficient or the coefficient of the squared term = 0 for a linear or quadratic regression of the variable as a function of inoculum density.

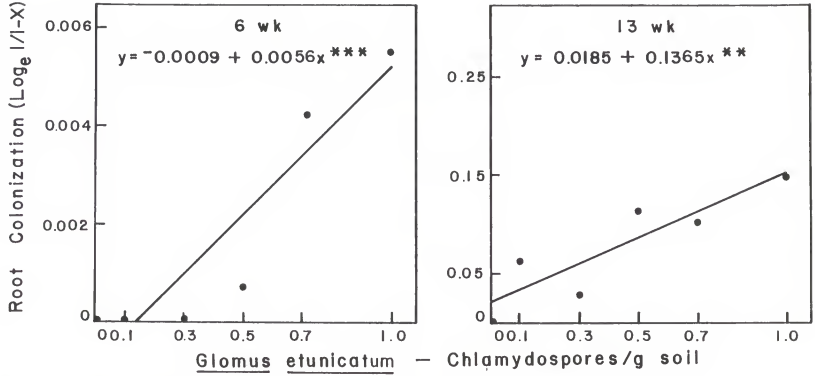

Fig. 3. The relationship of percentages of colonization of tomato (cv. Manapal) roots to initial densities of chlamydospores of G. etunicatum (Illinois isolate) 6 and 13 wk after seedling emergence, where seeds were planted in autoclaved infested soil. Prior to regression analysis, the data were transformed to Log_e 1/1-X, where X = proportion of intersects with mycorrhizal fungus root colonization as determined by a gridline intersect method described by Giovannetti and Mosse (1980). Equations calculated from 30 data points for each isolate x date combination are presented which possess a significant (***, **; $P < 0.001, < 0.01$) regression coefficient for rejection of the null hypothesis that the regression coefficient = 0 for a linear regression of the variable as a function of inoculum density.

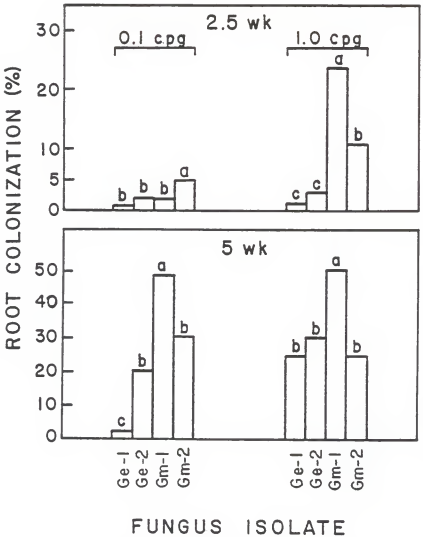

Fig. 4. Percent colonization as determined by a gridline intersect method described by Giovannetti and Mosse (1980) of tomato (cv. Manapal) roots by four isolates of mycorrhizal fungi (Ge-1 and Ge-2 = Glomus etunicatum, Illinois and Georgia, respectively; Gm-1 and Gm-2 = G. mosseae, Florida and England isolate, respectively). Data were collected 2.5 and 5 wk after seedling emergence, where seeds were planted in autoclaved soil infested with 0.1 and 1.0 chlamydospore of each isolate per gram dry soil (cpg). For each date x inoculum level combination, values followed by different letters are significantly different ($P < 0.05$) by Duncan's multiple range test.

Table 26. Means of tomato (cv. Manapal) growth, mycorrhizal fungus root colonization, and population density of two isolates each of Glomus etunicatum (Ge-1, Ge-2) and G. mosseae (Gm-1, Gm-2) of Experiment 1

Treatment	Shoot dry weight(g)		Root length(m)[t]		% Colonization[u]		Colonization index[v]		Population density(cpg)[w]	
	2.5 wk[x]	5 wk	2.5 wk	5 wk	2.5 wk	5 wk	2.5 wk	5 wk	2.5 wk	5 wk
Noninoculated	0.07[z]	1.10	0.27	8.50	0.00	0.00	0.00	0.00	0.0	0.0
Ge-1 (0.1)[y]	0.16	0.93	0.89	12.24	0.84	2.57	0.02	0.87	0.1	0.0
Ge-1 (1.0)	0.23	1.13	0.61	17.63	1.03	24.70	0.02	10.62	0.2	0.4
Ge-1 (10.0)	0.10	0.72	0.44	12.35	2.42	48.86	0.05	13.39	0.8	0.2
Ge-2 (0.1)	0.20	1.11	1.43	14.18	1.99	19.97	0.07	6.99	0.3	0.3
Ge-2 (1.0)	0.20	1.42	0.96	15.14	3.19	31.80	0.05	11.13	0.1	0.3
Ge-2 (10.0)	0.28	0.93	1.93	14.28	23.17	45.12	1.09	15.33	1.6	0.8
Gm-1 (0.1)	0.15	0.70	0.68	10.01	1.98	48.70	0.07	12.66	0.1	0.8
Gm-1 (1.0)	0.28	1.19	0.76	18.71	23.76	50.50	0.51	21.72	0.3	0.4
Gm-1 (10.0)	0.22	1.10	0.73	20.53	44.87	43.59	0.73	19.36	4.6	1.2
Gm-2 (0.1)	0.13	0.76	0.53	11.07	4.90	31.76	0.07	8.66	0.0	0.1
Gm-2 (1.0)	0.14	0.84	1.25	8.74	11.05	24.94	0.38	5.74	0.1	0.1

[t]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[u]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[v]Calculated by % Colonization x total root dry weight(g).
[w]Each value based on three replicates; cpg = chlamydospores per gram dry soil.
[x]Data collected 2.5 and 5 wk after seedling emergence.
[y]Chlamydospores of Ge-1, Ge-2 (Illinois and Georgia isolate, respectively) and Gm-1, Gm-2 (Florida and England isolate, respectively) added to autoclaved soil to achieve initial inoculum levels of 0.0, 0.1, 1.0, and 10.0 (except for Gm-2 at 10.0 cpg) cpg.
[z]Each value based on five replicates unless noted otherwise.

Table 27. Means of tomato (cv. Manapal) growth, mycorrhizal fungus root colonization, and population density of Glomus etunicatum (Ge) and G. mosseae (Gm) of Experiment 2

Treatment	Shoot height(cm)			Root length(m)[s]			% Colonization[t]			Colonization index[u]			Population density(cpg)[v]		
	2 wk[w]	6 wk	13 wk	2 wk	6 wk	13 wk	2 wk	6 wk	13 wk	2 wk	6 wk	13 wk	2 wk	6 wk	13 wk
Noninoculated	5.3[y]	37.6	NC[z]	NC	132	464	0.00	0.00	0.00	NC	0.00	0.00	0.00	0.00	0.01
Ge-1 (0.1)[x]	7.2	57.6	NC	NC	177	519	0.51	0.00	6.03	NC	0.00	24.98	0.04	0.00	4.34
Ge-1 (0.3)	7.0	58.6	NC	NC	194	665	0.11	0.00	2.82	NC	0.00	12.10	0.07	0.09	0.45
Ge-1 (0.5)	7.4	52.3	NC	NC	197	821	0.53	0.08	10.57	NC	0.14	50.38	0.12	0.03	2.34
Ge-1 (0.7)	7.5	55.8	NC	NC	223	738	0.16	0.42	9.49	NC	0.78	34.23	0.13	0.07	10.48
Ge-1 (1.0)	6.5	57.2	NC	NC	182	427	0.18	0.55	13.62	NC	0.85	38.56	0.20	0.09	19.89
Gm-1 (0.1)	5.5	34.4	NC	NC	134	354	0.28	0.21	11.71	NC	0.34	29.69	0.03	0.04	0.06
Gm-1 (0.3)	5.6	43.2	NC	NC	149	407	1.27	0.31	15.39	NC	0.49	39.98	0.09	0.09	0.62
Gm-1 (0.5)	5.9	46.0	NC	NC	160	320	0.77	1.07	18.70	NC	1.76	58.38	0.19	0.27	1.12
Gm-1 (0.7)	5.2	47.8	NC	NC	134	347	0.41	1.45	19.13	NC	1.68	48.96	0.20	0.23	0.85
Gm-1 (1.0)	5.2	48.4	NC	NC	286	476	1.31	1.63	18.39	NC	2.95	53.33	0.46	0.49	0.89

[s]Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).
[t]Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).
[u]Calculated by % Colonization x total root dry weight(g).
[v]Each value based on three replicates; cpg = chlamydospores per gram dry soil.
[w]Data collected 2, 6, and 13 wk after seedling emergence.
[x]Chlamydospores of Ge-1, Gm-1 (Illinois and Florida isolate, respectively) added to autoclaved soil to achieve initial inoculum levels of 0.0, 0.1, 0.3, 0.5, 0.7, and 1.0 cpg.
[y]Each value based on five replicates unless noted otherwise.
[z]Data not collected (NC).

Table 28. Means of tomato (cv. Manapal) growth, mycorrhizal fungus root colonization, and population density of Glomus etunicatum (Ge) and G. mosseae (Gm) of Experiment 3

Treatment	Shoot height (cm)				Root length (m)[s]				% Colonization[t]				No. colonization sites/plant[u]				Population density (cpg)[v]			
	Transplant[w]		Seed		Transplant		Seed		Transplant		Seed		Transplant		Seed		Transplant		Seed	
	6 wk[x]	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk	6 wk	8 wk
First performance																				
Noninoculated	34.6[z]	54.0	32.0	47.4	210	360	53	132	0.00	0.00	0.00	0.20	0	0	0	30	0.01	0.00	0.00	0.01
Ge-1 (0.1)[y]	32.3	47.9	32.7	40.0	202	371	29	134	0.75	0.98	2.34	1.00	143	368	52	146	0.01	0.00	0.03	0.07
Ge-1 (0.5)	47.0	50.0	31.7	41.5	193	371	66	125	0.72	2.58	0.39	1.64	145	793	26	215	0.05	0.03	0.06	0.12
Ge-1 (1.0)	42.9	65.9	31.6	41.7	240	351	90	160	1.45	3.32	0.73	1.48	386	1182	56	253	0.13	0.05	0.17	0.01
Gm-1 (0.1)	45.3	50.2	35.0	41.2	183	289	97	112	0.07	2.66	0.37	0.37	14	556	33	40	0.04	0.05	0.03	0.01
Gm-1 (0.5)	41.2	59.4	34.9	43.7	177	275	39	120	0.24	1.68	1.09	1.75	47	415	45	192	0.19	0.23	0.10	0.05
Gm-1 (1.0)	37.6	61.0	40.2	41.9	169	323	65	131	0.67	1.04	0.66	2.40	116	409	47	285	0.32	0.46	0.31	0.17
Second performance																				
Noninoculated	11.5	22.0	10.0	12.0	45	70	13	6	0.00	0.00	0.00	0.00	0	0	0	0	0.00	0.01	0.01	0.00
Ge-1 (0.1)	14.3	25.2	10.2	24.0	64	91	18	176	0.55	0.34	0.31	1.07	37	30	8	196	0.02	0.03	0.01	0.00
Ge-1 (0.5)	16.0	26.7	9.1	17.8	90	76	15	93	0.09	0.49	0.54	1.30	8	41	5	143	0.11	0.07	0.07	0.01
Ge-1 (1.0)	15.1	23.8	10.7	19.3	73	83	24	136	0.00	0.32	3.31	1.92	0	35	12	257	0.15	0.16	0.07	0.03
Gm-1 (0.1)	13.8	24.7	10.9	22.4	66	86	18	170	0.13	0.09	1.31	0.21	6	7	30	40	0.01	0.03	0.07	0.01
Gm-1 (0.5)	19.2	27.1	5.1	15.5	105	122	2	116	0.55	0.75	1.95	0.71	44	95	5	92	0.14	0.15	0.07	0.13
Gm-1 (1.0)	15.4	22.1	9.5	19.0	132	69	17	160	0.61	0.47	1.62	3.01	28	36	28	513	0.27	0.17	0.12	0.09

[s] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[t] Calcualted by a gridline intersect method (Giovannetti and Mosse, 1980).

[u] Calculated by no. of individual sites of colonization/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[v] Each value based on three replicates; cpg = chlamydospores per gram dry soil.

[w] Mycorrhizal or nonmycorrhizal transplant or seeds planted in infested or noninfested soil, respectively.

[x] Data collected 6 and 8 wk after transplanting or seeding.

[y] Chlamydospores of Ge-1, Gm-1 (Illinois and Florida isolate, respectively) added to autoclaved soil to achieve initial inoculum levels of 0.0, 0.1, 0.5, and 1.0 cpg.

[z] Each value based on five replicates unless noted otherwise.

Table 29. Significant linear and quadratic regression equations for tomato (cv. Manapal) growth and mycorrhizal fungus root colonization and population density as functions of initial inoculum levels of either Glomus etunicatum (Ge) or G. mosseae (Gm) in Experiment 1

Variable	Fungus species[q]	Harvest date[r]	Equation
Linear[s]			
% Colonization[t,u]	Ge-1	2.5 wk	$y = 0.0085 + 0.0016x^{xz}$
	Ge-2	2.5 wk	$y = 0.0133 + 0.0250x^{****}$
	Gm-1	2.5 wk	$y = 0.0861 + 0.0579x^{**}$
	Ge-1	5.0 wk	$y = 0.0938 + 0.0591x^{****}$
	Ge-2	5.0 wk	$y = 0.2836 + 0.3259x^{**}$
Colonization index[v]	Ge-2	2.5 wk	$y = -0.01 + 0.12x^{*}$
	Ge-1	5.0 wk	$y = 3.91 + 0.95x^{*}$
Population density (chlamydospores/ g dry soil)[w]	Ge-1	2.5 wk	$y = 0.07 + 0.07x^{*}$
	Ge-2	2.5 wk	$y = 0.09 + 0.13x^{*}$
	Gm-1	2.5 wk	$y = -0.03 + 0.46x^{***}$
Quadratic[x]			
Root length(m)[y]	Ge-1	5.0 wk	$y = 1866.1 + 771.7x - 74.5x^{2*}$
% Colonization	Ge-1	5.0 wk	$y = -0.0053 + 0.3179x - 0.0250x^{2**}$
Colonization index	Ge-1	5.0 wk	$y = -0.39 + 12.17x - 1.08x^{2**}$
	Gm-1	5.0 wk	$y = 11.94 + 10.93x - 1.02x^{2*}$

[q] Chlamydospores of Ge-1, Gm-1 (Illinois or Florida isolate, respectively) added to autoclaved soil to achieve initial inoculum levels of 0.0, 0.1, 1.0, and 10.0 chlamydospores per gram dry soil.

[r] Data collected at 2.5 and 5.0 wk after seedling emergence.

[s] Linear regression equations calculated from all data points (20, unless noted otherwise) for each isolate x date x variable combination are presented which possess a significant regression coefficient for rejection of the null hypothesis that the regression = 0 for a linear regression of the variable as a function of inoculum density.

[t] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980).

[u] Prior to regression % Colonization data were transformed to Log_e 1/1-X, where X = proportion of gridline intersects with mycorrhizal fungus root colonization.

[v] Calculated by % Colonization x total root dry weight(g).

[w] Regression equations based on 12 data points each.

[x] Quadratic regression equations calculated from all data points for each isolate x date x variable combination are presented which possess a significant coefficient of the squared term for rejection of the null hypothesis that the coefficient of the squared term = 0 for a quadratic regression of the variable as a function of inoculum density.

[z] *,**,**** Indicate the significance levels ($P < 0.05$, 0.01, 0.001, 0.0001, respectively) for the regression equations presented.

Table 30. Significant linear and quadratic regression equations for tomato (cv. Manapal) growth and mycorrhizal fungus development as functions of initial inoculum levels of Glomus etunicatum (Ge) and G. mosseae (Gm) in Experiment 2

Variable	Fungus species[p]	Harvest date[q]	Equation
Linear[r]			
Shoot dry weight(g)[s]	Gm-1	6 wk	$y = 2.47 + 1.56x^{***z}$
Root length(m)[t]	Gm-1	6 wk	$y = 130.5 + 131.6x^{**}$
% Colonization[u,v]	Ge-1	6 wk	$y = -0.0009 + 0.0056x^{***}$
	Gm-1	6 wk	$y = 0.00002 + 0.0181x^{***}$
	Ge-1	13 wk	$y = 0.0185 + 0.1365x^{**}$
	Gm-1	13 wk	$y = 0.0787 + 0.1752x^{**}$
Colonization index[w]	Ge-1	6 wk	$y = -0.13 + 0.87x^{****}$
	Gm-1	6 wk	$y = -0.05 + 2.88x^{***}$
	Ge-1	13 wk	$y = 11.90 + 35.02x^{*}$
	Gm-1	13 wk	$y = 18.99 + 44.77x^{**}$
Population density (chlamydospores/ g dry soil)[x]	Ge-1	2 wk	$y = 0.01 + 0.18x^{****}$
	Gm-1	2 wk	$y = -0.02 + 0.40x^{****}$
	Ge-1	6 wk	$y = 0.01 + 0.08x^{*}$
	Gm-1	6 wk	$y = -0.01 + 0.43x^{****}$
	Ge-1	13 wk	$y = -0.37 + 18.93x^{****}$
	Gm-1	13 wk	$y = 0.16 + 0.95x^{**}$
Quadratic[y]			
Shoot dry weight(g)	Ge-1	6 wk	$y = 0.32 + 4.09x - 8.18x^{2***}$
Root dry weight(g)	Ge-1	13 wk	$y = 3.44 + 5.63x - 5.58x^{2*}$
Root length(m)	Gm-1	6 wk	$y = 163.2 - 140.7x + 278.0x^{2*}$
% Colonization	Gm-1	13 wk	$y = 0.0314 + 0.5688x - 0.4018x^{2**}$
Colonization index	Ge-1	6 wk	$y = 0.01 - 0.35x + 1.19x^{2*}$
	Gm-1	13 wk	$y = 7.42 + 140.96x - 98.20x^{2*}$
Population density (chlamydospores/ g dry soil)	Gm-1	13 wk	$y = -3.59 + 144.94x - 99.60x^{2*}$

[q] Chlamydospores of Ge-1, Gm-1 (Illinois or Florida isolate, respectively) added to autoclaved soil to achieve initial inoculum levels of 0.0, 0.1, 0.3, 0.5, 0.7, and 1.0 chlamydospore per gram dry soil.

[r] Data collected 2, 6, and 13 wk after seedling emergence.

[s] Equations calculated from all data points (60 for 2 wk harvest, and 30 for 6 and 13 wk harvest, respectively) for each isolate x date x variable combination are presented possessing a significant coefficient for rejection of the null hypothesis that the regression coefficient = 0 for a linear regression of the variable as a function of inoculum density.

[t] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[u,v] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980); data were transformed to Log_e 1/1-X, where X = proportion of gridline intersects with mycorrhizal fungus root colonization.

[w] Calculated by % Colonization x total root dry weight(g).

[x] Regression equations based on 18 data points each.

[y] Quadratic regression equations calculated from all data points for each isolate x date x variable combination are presented possessing a significant coefficient of the squared term for rejection of the null hypothesis that the coefficient = 0 for a quadratic regression of the variable as a function of inoculum density.

[z] *, **, ***, **** Indicate the significance levels ($P < 0.05$, 0.01, 0.001, 0.0001, respectively) for the regression equations presented.

Table 3]. Significant linear and quadratic regression equations for tomato (cv. Manapal) growth and mycorrhizal fungus development as functions of initial inoculum levels of Glomus etunicatum (Ge) and G. mosseae (Gm) in Experiment 3

Variable	Fungus species[p]	Plant age at inoculation[q]	Experimental performance	Harvest Date[r]	Equation
Linear[s]					
Shoot height(cm)	Ge-1	transplant	first	8 wk	$y = 43.66 + 20.48x^{**z}$
	Gm-1	seed	first	6 wk	$y = 32.74 + 6.95x^{*}$
Root length(m)[t]	Ge-1	seed	first	6 wk	$y = 25.2 + 68.3x^{****}$
% Colonization[u,v]	Ge-1	transplant	first	8 wk	$y = 0.0094 + 0.0262x^{*}$
	Ge-1	transplant	second	6 wk	$y = 0.0053 - 0.0060x^{*}$
	Gm-1	transplant	first	6 wk	$y = -0.0001 + 0.0065x^{**}$
	Gm-1	seed	first	8 wk	$y = 0.0026 + 0.0233x^{**}$
	Gm-1	transplant	second	6 wk	$y = 0.0007 + 0.0064x^{**}$
	Gm-1	seed	second	8 wk	$y = -0.0028 + 0.0310x^{**}$
No. colonization sites/plant[w]	Ge-1	transplant	first	8 wk	$y = 301.4 + 899.3x^{**}$
	Gm-1	transplant	first	6 wk	$y = -0.976 + 113.1x^{**}$
	Gm-1	seed	first	8 wk	$y = 29.52 + 268.06x^{**}$
	Gm-1	transplant	second	6 wk	$y = 6.71 + 33.21x^{*}$
	Gm-1	seed	second	8 wk	$y = -72.21 + 538.52x^{*}$
Population density (chlamydospore g dry soil)[x]	Ge-1	transplant	first	6 wk	$y = -0.0032 + 0.1268x^{**}$
	Ge-1	transplant	first	8 wk	$y = -0.0030 + 0.0514x^{*}$
	Ge-1	transplant	second	6 wk	$y = 0.0174 + 0.1388x^{*}$
	Ge-1	transplant	second	8 wk	$y = 0.0071 + 0.1492x^{*}$
	Gm-1	transplant	first	6 wk	$y = 0.0131 + 0.3173x^{****}$
	Gm-1	seed	first	6 wk	$y = -0.0096 \pm 0.3032x^{****}$
	Gm-1	seed	first	8 wk	$y = -0.0088 + 0.1677x^{****}$
	Gm-1	transplant	second	6 wk	$y = -0.0076 + 0.2774x^{**}$
	Gm-1	transplant	second	8 wk	$y = 0.233 + 0.1710x^{**}$
	Gm-1	seed	second	6 wk	$y = 0.0323 + 0.08x^{**}$
	Gm-1	seed	second	8 wk	$y = 0.0166 + 0.1043x^{*}$
Quadratic[y]					
Shoot height(cm)	Ge-1	transplant	first	6 wk	$y = 26.13 + 66.72x - 49.94x^{2*}$
	Gm-1	transplant	second	6 wk	$y = 1143 + 26.96x - 22.98x^{2*}$
	Gm-1	seed	second	8 wk	$y = 11.74 - 22.86x + 20.54x^{2*}$
Root length(m)	Ge-1	seed	second	8 wk	$y = 212.5 - 400.3 + 323.6x^{2*}$
	Gm-1	transplant	second	8 wk	$y = 68.7 + 210.3x - 209.7x^{2**}$
% Colonization	Gm-1	seeds	first	6 wk	$y = 0.0001 + 0.0370x - 0.0305x^{2**}$
No. colonization sites/plant	Gm-1	transplant	second	6 wk	$y = -3.32 + 151.36x - 120.08x^{2*}$
Population density (chlamydospore g dry soil)	Ge-1	seed	first	8 wk	$y = 0.04 + 0.35x - 0.38x^{2*}$
	Gm-1	seed	second	8 wk	$y = -0.01 + 0.42x - 0.32x^{2*}$

[p] Chlamydospores of Ge-1, Gm-1 (Illinois and Florida isolate, respectively) added to autoclaved soil to achieve initial inoculum levels of 0.0, 0.1, 0.5, and 1.0 chlamydospore per gram dry soil.

[q] Mycorrhizal or nonmycorrhizal transplants or seeds planted in infested or non-infested soil, respectively.

[r] Data collected 6 and 8 wk after transplanting or seeding.

[s] Equations calculated from 20 data points for each isolate x date x variable combination are presented possessing a significant coefficient for rejection of the null hypothesis that the regression coefficient = 0 for a linear regression of the variable as a function of inoculum density.

[t] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

Table 31--continued.

[u,v] Calculated by a gridline intersect method (Giovannetti and Mosse, 1980); data were transformed to Log_e 1/1-X, where X = proportion of gridline intersects with mycorrhizal fungus root colonization.

[w] Calculated by no. of colonization sites/0.5g root fresh weight x root dry weight x total root dry weight(g).

[x] Regression equations based on 12 data points.

[y] Equations calculated from 20 points for each isolate and variable combination are presented possessing a significant coefficient of the squared term for rejection of the null hypothesis that the coefficient = 0 for a quadratic regression of the variable as a function of inoculum density.

[z] *, **, **** Indicate the significance levels ($P < 0.05$, 0.01, 0.0001, respectively) for the regression equations presented.

Discussion

Increases in levels of spore inoculum of mycorrhizal fungi in the range of those in field soils resulted in significant increases in colonization of tomato roots in each of the three experiments. Increasing levels of inoculum of Ge-1, Ge-2, and Gm-1 in the range of 0.1 to 10.0 cpg resulted in significant increases ($P < 0.05$ by linear regression analysis) in root colonization in Experiment 1. Additionally root colonization by Gm-2 increased with an increase in ID from 0.1 to 1.0 cpg at 2.5 wk but not at 5 wk after seedling emergence. In Experiment 2 increasing IDs of Ge-1 and Gm-1 in the range of 0.1 to 1.0 cpg increased root colonization although colonization levels generally were lower compared with those in Experiment 1. Spread of fungus growth within tomato roots was restricted at both dates in Experiment 3; however, increasing IDs of Ge-1 and Gm-1 in the range of 0.1 to 1.0 cpg resulted in significant increases in root colonization for both plant age types (transplants, seeds) evaluated.

Use of the CI variable resulted in similar detections of ID:fungus growth relationships compared with the root colonization variable in Experiments 1 and 2. Similarly in Experiment 3, use of the number of colonization sites variable provided similar detections of relationships between fungus growth as a function of ID as did the root colonization variable. Both the CI and the number of colonization sites variables are calculated as functions of root dry weight. Increases in root dry weight as ID increased could have decreased the percent of root colonization. Theoretically making adjustments in fungus growth by considering differences in root dry weight could enable differences in total fungus growth to be detected. In that root dry weight rarely increased significantly

with ID, no apparent advantage was perceived in using the CI and the number of colonization sites variables.

Both species and each of the four isolates tested resulted in significant increases in root colonization as ID increased. Specific levels of colonization varied by species and isolate. Over Experiments 1 and 2, when colonization levels were higher than in Experiment 3, Gm-1 had significantly greater ($P < 0.01$, 21 pairs, by Wilcoxon's signed rank test) root colonization (%) values than Ge-1 for each ID tested. Similarly Gm-1 had significantly higher ($P < 0.05$ by Duncan's multiple range test) root colonization than Ge-2 and Gm-2 at 0.1 and 1.0 cpg at 5 wk after seedling emergence in Experiment 1. The regression slope of root colonization by Ge-2 as a function of ID was significantly steeper ($P < 0.01$ by Student's t-test, 38 d.f.) compared with that of Ge-1 in Experiment 1. If differences exist between species for the effectiveness at improving plant growth (Abbott and Robson, 1977, 1978; Carling and Brown, 1980; Daniels and Menge, 1981; McGraw and Schenck, 1980; Mosse, 1972a, 1972b), then it might be expected that differences in levels and/or rates of root colonization at equivalent IDs could be detected, as they were in this study. Daniels and McCool (1980) found similarly that differences in colonization of sudangrass varied between six isolates tested at equivalent IDs. Plant growth as a function of ID was not evaluated in their study. Further research is necessary to define what mechanisms for improved plant growth are in operation as the development of a mycorrhizal fungus in the root spreads both internally and externally.

Saturation effects (where significant quadratic regression equations were calculated) of fungus and plant growth as functions of ID

occurred occasionally. Increasing ID resulted in a less than proportionate increase in fungus and plant growth only at the final evaluation date in Experiment 1. Root colonization values at 5 wk after seedling emergence in Experiment 1 exceeded those in Experiments 2 and 3 at any date evaluated. Saturation effects of fungus and plant growth as functions of ID were detected 6 and 13 wk after seedling emergence in Experiment 2, and 6 and 8 wk after transplanting or seeding in Experiment 3. In that colonization values were low at both 6 and 8 wk in Experiment 3, it is unlikely that a threshold level of root colonization is necessary for detection of a saturation effect. It is conceivable that a significant period of time after inoculation, in addition to the amount of colonization detected, are necessary for relationships between ID and fungus growth to be detected. Further research is necessary to determine ID:fungus and plant growth relationships when the range of inoculum levels and root colonization values are both low and high.

Root colonization levels varied in each experiment. Generally colonization by a mycorrhizal fungus was highest in Experiment 1 and lowest in Experiment 3. The highest colonization values for Gm-1 were 50%, 19%, and 3% in Experiments 1, 2, and 3, respectively. Primary differences in methodology between experiments were 1) use of 10.2-cm-diameter clay pots in Experiment 1 compared with 15.2-cm-diameter plastic pots in Experiments 2 and 3. The clay pots may have altered the soil environment (ambient gas concentrations, soil moisture, soil temperature) in favor of active growth of the mycorrhizal fungi. Additionally the smaller diameter of the clay pots could have interacted with the soil environment, either qualitatively or quantitatively, thereby influencing

indirectly root colonization by the fungi. Activity of the fungi could have declined with length of time in storage. However, in an earlier study where root inoculum had been stored less that 1 month (McGraw and Schenck, 1980), levels of tomato (cv. Walter) root colonization by Gm-1 and Ge-1 were similar to those in Experiment 2 where inoculum had been stored for 6 months prior to use. In the earlier study, the ID used was approximately 0.3 cpg, and at 6.5, 8.5, 13, and 17 wk after inoculation, Gm-1 had colonization levels of 6.0, 15.0, 22.0, and 39.0%, respectively. In Experiment 2 Gm-1 and Ge-1 at 0.3 cpg had 3 and 15% root colonization, respectively at 13 wk after seedling emergence. Storage of spore inoculum in soil for up to 4 months did not reduce spore germination (Daniels and Trappe, 1979), therefore it is unlikely that differences in root colonization between experiments are due primarily to the length of time inoculum was stored in this study; other unknown factors also may have been involved.

As early as 2.5 wk after seedling emergence in Experiment 1, root colonization increased significantly with increasing ID. This relationship was not detected in Experiment 2 until 6 wk after seedling emergence. In Experiment 3 where fungus growth was restricted to individual entry-points into the root, significant ID:fungus growth relationships were detected 6 wk after transplanting or seeding. In that root colonization levels in Experiment 2 at 2 wk after seedling emergence were similar to colonization levels in Experiment 3 at 6 wk after transplanting or seeding, it is unclear why ID:fungus growth relationships were not detected in Experiment 2 for the first evaluation date. Possibly an insufficient period of time after inoculation had occurred for relationships to be detected.

Population densities of chlamydospores recovered from infested soils were related linearly to initial IDs. Generally populations were greater for Gm-1 compared with Ge-1 at early evaluation dates. However, populations at early dates for either Gm-1 or Ge-1 did not exceed those of the initial IDs. In contrast with population densities, Gm-1 had greater levels of root colonization than Ge-1, as was discussed previously. These relationships between ID and population density or fungus growth can be interpreted to mean that 1) Gm-1 is more effective than Ge-1 at colonizing roots per spore; or 2) initial IDs of Ge-1 were overestimated. If one assumes that all spores which were added were viable and were recovered with equal precision for each species, then it is possible that Gm-1 is more effective than Ge-1 in colonizing roots on a per spore basis. The mean spore diameter of G. mosseae is approximately twice that of G. etunicatum. A larger-spored species may have a greater supply of nutrient reserves available for spore germination, increased probability for root contact as a result of more extensive growth through the soil, and increased ability to penetrate and colonize roots. Daniels and McCool (1980) reported that G. mosseae had at least twice the "inoculum potential" of four small-spored species and isolates. Alternatively IDs of G. etunicatum could have been overestimated for several reasons. In that routine methods for determining spore viability of mycorrhizal fungi are not available, it is possible that a lesser proportion of spores of Ge-1 in the initial IDs were capable of germinating compared with spores of Gm-1. Additionally spores of G. etunicatum may be more susceptible to hyperparasitism and other degradation processes which occur in the soil environment. The fact that G. mosseae can colonize roots to a greater extent, and can improve plant growth above that of

other species (Daniels and Menge, 1981; McGraw and Schenck, 1980) could provide a tool for increasing root inoculum more efficiently. Source of spore inoculum often can be limiting for experimental purposes, and use of root inoculum might provide a suitable source of inoculum, particularly if routine procedures can be developed, such as those by Abbott and Robson (1981), for quantifying relationships between both root inoculum and fungus and plant growth. Root-fungus inoculum is thought to result in earlier root colonization than spore inoculum (Powell, 1976; Tommerup and Abbott, 1981).

Relationships between vegetative shoot or root growth and ID occurred rarely. Daft and Nicolson (1969) reported similarly that relationships between ID and tomato growth did not occur at 10 wk after inoculation when spores of G. macrocarpum were increased from 3 to 225 spores per plant. Carling et al. (1970) hypothesized that if samples had been taken before the 10 wk date, relationships could have been detected. However, results in this study conflict with that hypothesis. Possibly at lower IDs than those used in these studies, such as in field soils when inoculum becomes limiting following agricultural management practices (fumigation, cropping), ID:plant growth relationships may exist. A minimum ID of a mycorrhizal fungus at which plant growth is effected has not been established for any crop species.

Relationships between ID and fungus growth may be considered in a similar manner as relationships of ID and disease incidence or disease severity for soilborne fungal plant pathogens, since mycorrhizal fungus growth (colonization) was increased with increasing ID. Increasing our understanding of these relationships could facilitate the use of VA mycorrhizal fungi to increase crop productivity.

APPENDIX 1

THE DEVELOPMENT OF FUSARIUM WILT OF TOMATO (CULTIVAR RHEINGLUT) AS INFLUENCED BY THE VESICULAR-ARBUSCULAR MYCORRHIZAL FUNGUS, GLOMUS MOSSEAE

Introduction

The development of Fusarium wilt of tomato (Lycopersicon esculentum Mill. 'Manapal') as influenced by vesicular-arbuscular mycorrhizal fungi was described in Part 1 of this dissertation. Dual inoculations with the wilt fungus (Fusarium oxysporum Schlecht. f. sp. lycopersici (Sacc.) Snyd. & Hans. race 2 [Fol]) and either of two species of mycorrhizal fungi (Glomus etunicatum Becker & Gerd. or G. mosseae (Nicol. & Gerd.) Gerd. & Trappe resulted in earlier disease development compared with nonmycorrhizal plants inoculated with the wilt fungus. The earlier time to development of the wilt disease associated with the mycorrhizal fungi occurred when either transplants or seeds were inoculated dually. Disease severity (DS) was influenced by the mycorrhizal fungi as well as by a phosphorus (PO_4) amendment. Both a PO_4 amendment and inoculations with mycorrhizal fungi reduced disease expression; however, the relative degree of reduction differed between the treatments. Disease severity in plants inoculated with Fol was least with PO_4 amendments, intermediate with either mycorrhizal fungus, and greatest with Fol alone. Whether each mycorrhizal fungus decreased DS depended on which Fol control (with or without PO_4) was used for comparison. Mechanisms other than improved plant phosphorus nutrition may have been involved in the reduction in DS associated with the mycorrhizal fungi.

Dehne (1977) and Dehne and Schönbeck (1975) observed decreased wilt in tomato (L. Lycopersicum L. Karst. ex. Farw. = L. esculentum Mill. 'Rheinglut') preinoculated with G. mosseae and challenged subsequently by race 1 of the wilt fungus. Differences between treatments in the time of onset of disease were not evaluated in their study.

The objective of this study was to determine if in general the patterns of disease development and DS using the cultivar Rheinglut were similar to those described in Part 1 of this dissertation when the tomato cultivar Manapal was used. The mycorrhizal fungus, G. mosseae, and the tomato cultivar, Rheinglut, were selected for experimentation to allow comparisons with results presented both in Part 1 of this dissertation by Dehne (1977) and Dehne and Schönbeck (1975).

Materials and Methods

The procedures and methods used for fungal inoculum production, inoculum collection, and inoculation were identical to those utilized in Part 1 of this dissertation. A single mycorrhizal fungus species, G. mosseae (Gm; Florida isolate), was used at a single inoculum level (one chlamydospore per gram of soil [cpg]). An inoculum level of 500 cpg of race 2 of the wilt fungus was used for inoculation. Inoculations were made using 2-wk-old transplants (noninoculated or preinoculated with G. mosseae) of the cultivar Rheinglut (seeds obtained from H.-W. Dehne) and plants were grown as described in Part 1 of this dissertation. Plant and fungus growth and development were assessed 8 wk after inoculation and data were analyzed statistically by analysis of variance and by Duncan's multiple range test. The 8-wk assay date was selected to allow for both adequate time for disease development (when disease was not found 6 wk after inoculation) and for comparisons between experiments described in Part 1 of this dissertation, and the experiment described in this study. The experiment was conducted under greenhouse conditions concurrently with the second performance of the transplant experiment described in Part 1 of this dissertation. The experiment was conducted once with three replicate plants per treatment.

Results

The time to development of chlorosis and wilt did not occur until 6 wk after inoculation, at which time only one of three plants from a single treatment (Fol + PO_4) exhibited symptoms. At 8 wk after inoculation, DS was significantly greater ($P < 0.05$) for plants inoculated with the wilt fungus and amended with PO_4 than for plants in all other treatments (Table 32).

Root colonization by G. mosseae was limited to individual sites of hyphal penetration in the root cortex with few surrounding cells invaded. This type of development also was found in the experiment conducted concurrently (second performance of the transplant experiment described in Part 1 of this dissertation). Glomus mosseae colonized a significantly greater ($P < 0.05$) percentage of root length and initiated a greater number of colonization sites per plant in the presence compared with the absence of the wilt fungus.

Plant growth was not affected significantly by any fungus treatment. However, there was a tendency toward decreased shoot height and root length in plants inoculated dually with G. mosseae and Fol compared with plants in all other treatments.

Propagules of both G. mosseae and F. oxysporum were recovered from soil which had not been infested. However, spore numbers of G. mosseae in noninoculated treatments were significantly less than those in treatments which involved inoculations with the mycorrhizal fungus. Propagule population densities of F. oxysporum were lower in noninoculated treatments compared with densities in inoculated treatments. The highest densities were found in treatments where Fol alone was added.

Table 32. The effect of planting tomato (cv. Rheinglut) transplants in soil infested with Glomus mosseae (Gm) and/or with Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on the development of Fusarium wilt and on plant and fungus growth 8 wk after infestation

Treatment[r]	Shoot		Root		Population density (ppg)[t,u]		Mycorrhizal colonization		Disease
	dry weight (g)	height (cm)	dry weight (g)	length (m)[s]	mycorrhizal fungi	F. oxysporum	sites/plant[v]	%[w]	severity[x]
Noninoculated	1.41 a[y,z]	23.5 a	0.59 a	52.7 a	0.03 c	2.93 a	0 b	0.00 b	0.0 b
Noninoculated + PO_4	1.88 a	22.2 a	0.71 a	78.3 a	0.01 c	2.18 b	0 b	0.00 b	0.0 b
Gm	1.48 a	22.3 a	0.67 a	72.2 a	0.43 b	3.19 a	62 b	0.83 b	0.0 b
Gm + Fol	1.16 a	19.0 a	0.47 a	47.6 a	0.63 a	3.34 a	170 a	4.23 a	0.0 b
Fol	1.03 a	22.8 a	0.50 a	59.8 a	0.00 c	3.64 a	0 b	0.00 b	0.0 b
Fol + PO_4	1.18 a	22.5 a	0.47 a	69.2 a	0.00 c	3.78 a	0 b	0.00 b	1.0 a

[r] Plants grown in noninfested soil (noninoculated) (+ PO_4, phosphorus) or in soil infested with Gm at 1.0 chlamydospore per g of soil (cpg) and/or with Fol at 500 cpg.

[s] Calculated by root length(m)/0.5g root fresh weight x root dry weight constant x total root dry weight(g).

[t] Chlamydospores per g dry soil determined from three 50-g soil samples per treatment.

[u] Propagule population density per g dry soil (ppg) determined by soil dilution-plating on a selective medium; each value represents the mean of two (5-plate) samples: statistical analysis performed on a logarithmic transformation (Log_{10} (colony forming units/g + 1)) of the data; transformed data presented.

[v] Calculated by no. of individual colonization sites/0.5g root fresh wieght x root dry weight constant x total root dry weight(g).

[w] Determined by a gridline intersect method (Giovannetti and Mosse, 1980).

[x] Rating based on a scale of 0-4, where 0 = no symptoms, and 4 = 100% of the shoot exhibiting chlorosis, wilt, and/or necrosis.

[y] Each value represents the mean of three replications.

[z] Numbers in the same column followed by the same letter do not differ significantly ($P < 0.05$) by Duncan's multiple range test.

Discussion

The results of this experiment contrast in some ways with those described in Part 1 of this dissertation. Whereas symptom expression on Manapal occurred as early as 20 days and no later than 33 days after inoculation, no symptoms were observed on Rheinglut 8 wk after inoculation. The absence of disease symptoms (and minimal DS) 8 wk after inoculation in the majority of plants inoculated with Fol can be interpreted to mean that either 1) the cultivar Rheinglut was not susceptible to the race 2 isolate of the wilt fungus used under the conditions provided in this study; or 2) the isolate of the wilt fungus used no longer was pathogenic. Evidence for pathogenicity of the wilt fungus isolate was confirmed in the experiment conducted concurrently, where inoculum of Fol used was from the same preparation as that used in this study. Alternatively the host cultivar used in this study may have been resistant to disease expression. The fact that the cultivar Rheinglut was bred in West Germany, possibly under dissimilar environmental conditions as those utilized for the Florida-bred cultivar Manapal, may support this suggestion.

Compared with plants inoculated with Fol alone, dual inoculation with G. mosseae and Fol resulted in significantly increased levels of root colonization and numbers of colonization sites per plant by G. mosseae, increased populations of chlamydospores of G. mosseae recovered, and a tendency toward reduced shoot height and root length. Apparently the development of mycorrhizae was favored by the presence of the wilt fungus. Enhancement of mycorrhizal fungus root colonization by Fol probably was initiated after spore germination and root contact by G. mosseae. The higher numbers of recovered spores in the dual inoculation treatment

(none of which exceeded the initial inoculum level for G. mosseae) implies that fewer spores germinated or contacted the root. The wilt fungus could have altered the physiology of the host, particularly of the roots (e.g., root exudates [Graham et al., 1981]), in such a way as to support increased penetration of G. mosseae.

Results from this study differ from those reported by Dehne (1977) and Dehne and Schönbeck (1975). They found that disease occurred in plants inoculated with Fol, although disease expression was less when plants were inoculated dually with G. mosseae and the wilt fungus compared with plants inoculated with Fol alone. If anything, plant growth in this study appeared to be influenced negatively by dual inoculation, although plant growth was not affected significantly by inoculations with the respective fungi.

As has been suggested earlier in Part 1 of this dissertation, comparisons of results from different reports may not be possible unless care is taken to duplicate the experimental conditions. Differing conditions between those described in this study and those of Dehne (1977) and Dehne and Schönbeck (1975) may explain the differences in results. In contrast to this study, Dehne (1977) and Dehne and Schönbeck (1975) used a different isolate of G. mosseae and a different race (race 1) of the pathogen; utilized conidia of the wilt fungus as inoculum (a propagule not considered to be the primary survival structure of Fusarium spp. Nash et al., (1961) ; observed the occurrence of extensive spread of root colonization by the mycorrhizal fungus; and used sand as the plant growth medium. Each of these differences could influence disease development. In a subsequent study (described in Appendix 2 of this dissertation), growth medium (sand, soil) had a significant influence

on the development of Fusarium wilt in the cultivar Manapal, as influenced by G. mosseae. The time of onset of disease symptoms occurred earlier when plants were grown in sand compared with soil although final disease expression was more severe in plants grown in soil, regardless of the inoculant.

The implications of these findings are that the outcome of disease interactions may vary with the experimental conditions employed. Generalizations should not be made regarding the influence mycorrhizae have on plant diseases, except to state that mycorrhizae either can be non-influential or can influence plant disease expression.

APPENDIX 2

THE INFLUENCE OF GROWTH MEDIA AND GLOMUS MOSSEAE ON THE DEVELOPMENT OF FUSARIUM WILT OF TOMATO (CULTIVAR MANAPAL)

Introduction

The influence of vesicular-arbuscular mycorrhizal fungi on the development of Fusarium wilt of tomato was described in Part 1 and Appendix 1 of this dissertation. The time to onset of disease symptoms occurred earlier in plants inoculated dually with a mycorrhizal fungus and the wilt fungus compared with plants inoculated with the wilt fungus alone, when the tomato (Lycopersicon esculentum Mill.) cultivar Manapal was used. Disease was sporadic in plants inoculated with the pathogen when the cultivar Rheinglut was used. In contrast Dehne (1977) and Dehne and Schönbeck (1975) noted disease expression in tomato (cv. Rheinglut) plants inoculated with the wilt fungus, but observed a decrease in wilt in mycorrhizal plants preinoculated with Glomus mosseae (Nicol. & Gerd.) Gerd. & Trappe and subsequently challenged by the wilt fungus. The disparity in results of these studies may be due to differences in host cultivar, plant growth media, race of the pathogen, type of propagule of the pathogen, and/or host growing conditions (refer to Appendix 1 of this dissertation for a discussion of these differences). The objective of this study was to ascertain the effects of growth medium on the development of Fusarium wilt of tomato (cv. Manapal) as influenced by the mycorrhizal fungus, G. mosseae.

Materials and Methods

The proceduees and methods used for fungal inoculum production, inoculum collection, and inoculation were identical to those described in Part 1 of this dissertation. Inoculum levels used were 1.0 chlamydospore per gram of growth medium (cpg) of G. mosseae and 500 cpg of Fusarium oxysporum Schlecht. f. sp. lycopersici (Sacc.) Snyd. & Hans. race 2 (Fol). Sixty grams of noninfested or infested soil or acid-washed builder's sand were added to 50-ml polypropylene beakers. The sand had been soaked in 12 N hydrochloric acid for 12 hr, rinsed in deionized water for 1 hr, and rinsed in tap water for 4 hr. Three surface-disinfected (10 min in 0.525% sodium hypochlorite followed by three rinses in sterile deionized water) seeds of the tomato cultivar Manapal were planted in each beaker. Beakers were placed in nylon trays and were maintained in a growth chamber at 25 C and 12 hr light (4000 lux) per day for 3 wk. Plants were watered daily and fertilized (10 ml/beaker/week) with full-strength Hoagland's solution (Hoagland and Arnon, 1938), with or without phosphorus (PO_4).

Plants in each of five beakers per treatment were evaluated 3 wk after inoculation, and disease severity (DS) as well as propagule population densities of F. oxysporum in both growth media were assessed using the procedures and methods described in Part 1 of this dissertation. Data were analyzed statistically by analysis of variance and by Duncan's multiple range test.

Results

Disease symptoms (chlorosis and wilt) first were observed 10 and 14 days after planting seeds in sand and soil media, respectively, infested with Fol. The earliest time of onset of disease symptoms (data not presented) and the highest DS values in plants grown in either medium occurred in plants inoculated with the pathogen alone (with or without PO_4) compared with plants in all other treatments (Table 33). Similarly in a preliminary experiment where sand only was used, disease symptoms developed by 12 days after inoculation and DS was greatest in plants inoculated with the wilt fungus alone (data not presented). Disease severity 3 wk after inoculation was higher in plants grown in soil compared with plants grown in sand.

Populations of F. oxysporum detected in growth media which had been infested with G. mosseae but not with the wilt fungus were not significantly different compared with populations in growth media to which the pathogen alone had been added. Significantly fewer ($P < 0.05$) propagules of F. oxysporum were detected in the noninfested soil but not in the sand compared with infested soil or sand growth media, respectively, regardless of the fungus added.

The addition of PO_4 increased DS in nonmycorrhizal plants inoculated with the pathogen when plants were grown in soil but not when plants were grown in sand. Lower levels of F. oxysporum propagules were detected from either media where PO_4 amendments were applied to plants inoculated with Fol compared with plants inoculated with Fol alone where PO_4 was withheld.

Table 33. The effect of growth media on disease severity of Fusarium wilt of tomato (cultivar Manapal) and on populations of Fusarium oxysporum in the growth medium where plants were grown in noninfested soil or in soil infested with Glomus mosseae (Gm) and/or with F. oxysporum f. sp. lycopersici race 2 (Fol)

Treatment	Disease severity[t,u,v,w]		Fol population density (ppg)[z]	
	sand[x]	soil[y]	sand	soil
Noninoculated	0.0 c	0.0 c	0.00 d	1.11 d
Noninoculated + PO_4	0.0 c	0.0 c	1.40 d	0.00 d
Gm	0.0 c	0.0 c	2.74 cd	3.77 a
Gm + Fol	0.0 c	0.4 c	2.95 cd	3.56 abc
Fol	2.0 b	2.8 b	3.44 bcd	3.72 ab
Fol + PO_4	2.0 b	4.0 a	3.02 cd	3.63 ab

[s] Plants were grown in noninfested (noninoculated with or without PO_4) soil or were grown in media infested with Gm and/or Fol (with or without PO_4) at 1.0 or 500 chlamydospores per g soil (cpg) respectively.
[t] Data were collected at 3 wk after infestation.
[u] Based on a scale of 0-4, where 0 = no symptoms, and 4 = 100% of shoot exhibiting symptoms of chlorosis, wilt, and/or necrosis.
[v] Values represents the mean of five replications, unless noted otherwise.
[w] Numbers for each variable followed by the same letter do not differ significantly ($P < 0.05$) by Duncan's multiple range test.
[x] Acid-washed builder's sand.
[y] Autoclaved Lakeland fine sand.
[z] Based on plating soil dilutions on a selective medium; values represent the mean of two replicate (five plates per replicate) samples; transformed (Log_{10} (colony forming units/g + 1)) data analyzed and presented.

Discussion

The effect of growth medium on the outcome of the disease interaction was marked. The time of onset of disease symptoms occurred four days earlier in plants inoculated with the wilt fungus alone and grown in sand than in plants inoculated similarly and grown in soil. However, DS was significantly greater ($P < 0.05$) 3 wk after inoculation in plants which were inoculated with the wilt fungus alone, received PO_4 amendments, and were grown in soil compared with similarly inoculated plants grown in sand. Similarly DS was greater, although not significantly so, in plants inoculated with the wilt fungus alone (in the absence of PO_4) and grown in soil compared with sand.

Disease severity eventually became more severe in inoculated plants in the soil compared with the sand medium. It is possible that nutrients became limiting to the development of the wilt fungus earlier in the sand compared with the soil medium resulting in earlier disease onset as the pathogen switched to utilizing the plant as a substrate. Comparatively higher populations of microflora in the soil which were antagonistic to the wilt fungus, where total substrates undoubtedly were in greater availability, compared with populations in the sand medium could have limited the activity of the wilt fungus initially. However, the greater amount of substrate in the soil environment may have enabled populations of the pathogen to increase to a significantly greater extent than those in the sand medium as was observed in this study. The higher populations of F. oxysporum in soil could have resulted in higher DS in inoculated plants grown in soil compared with those grown in sand.

The enhancement of DS by the PO_4 amendment to plants inoculated with

the wilt fungus supports the suggestion that increased nutrients for the wilt fungus can result in greater DS in inoculated plants grown in the soil compared with sand growth medium. However, this suggestion conflicts with the results presented in Part 1 of this dissertation, in which PO_4 amendments reduced DS of Fusarium wilt. This phenomonon was attributed to improved host phosphorus nutrition, which could have acted to limit the development of the disease. Different environmental conditions in the greenhouse (used in the experiments in Part 1) compared with the growth chamber (used in the study described herein) could have influenced the development of the disease (Jones and Woltz, 1969).

The absence (or very limited development) of disease in plants inoculated with G. mosseae and Fol, regardless of the use of either sand or soil growth medium, conflicts with results obtained in a greenhouse study described in Part 1 of this dissertation, where disease developed extensively in plants inoculated dually when the culitvar Manapal was used. However, in another study (reported in Appendix 1 of this dissertation), dual inoculations using the cultivar Rheinglut resulted in disease only when plants were inoculated with the wilt fungus alone and additionally received PO_4 amendments. As suggested above pronounced differences in environmental conditions in the greenhouse compared with growth chamber could have influenced disease development. The constant wetting and drying of the growth media as well as differing quality and quantity of light could have stressed plant growth more in the growth chamber than in the greenhouse. This increased plant stress could have enhanced the activity of the wilt fungus (Walker, 1971).

Inoculating with G. mosseae resulted in less disease in plants when plants were grown in the growth chamber. Two possible

mechanisms for protection include 1) direct protection by a fungal (mycorrhizal) barrier, such as could exist if root colonization by the mycorrhizal fungus occurred; or 2) indirect protection by altered host physiology. Results from a previous experiment conducted in a growth chamber indicated that mycorrhizal fungus colonization sites in Manapal tomato occurred as early as seven days after planting germinated seeds in soil infested with 0.1, 0.5, 1.0, and 5.0 cpg of G. mosseae (data not presented). The incidence of occurrence of root colonization at any of the inoculum levels tested did not exceed 12%, and by 21 days after planting, incidence remained 12% or less. Therefore it is doubtful if direct protection from the wilt fungus by a physical barrier by G. mosseae occurred. A more likely alternative could be that a physiologically induced protection mechanism occurred. Altered host physiology could have decreased susceptibility to root infection by the pathogen either directly or indirectly.

Further research is needed to evaluate more thoroughly the influence of growth media and environmental conditions on the development of Fusarium wilt of tomato as influenced by mycorrhizal fungi. It seems likely that the choice of either sand or soil media for growing tomato plants could influence disease development. Additionally as noted previously (Part 1 and Appendix 1 of this dissertation), standardization of methods is an important aspect of making comparisons between studies.

APPENDIX 3

EFFECT OF INOCULATION OF TOMATO (CULTIVAR MANAPAL) WITH MYCORRHIZAL FUNGI AND THE FUSARIUM WILT FUNGUS ON CHEMICAL ELEMENTS IN PLANT TISSUE

Introduction

Increased mineral absorption by mycorrhizal roots and root colonization by mycorrhizal fungi can influence diseases caused by soilborne fungi (Schenck and Kellam, 1978). Internal concentrations of phosphorus (PO_4) in plant tissues have been emphasized as affecting disease interactions involving vesicular-arbuscular mycorrhizal fungi. Graham and coworkers (1981) suggest that internal PO_4 concentrations may regulate mycorrhizal fungus colonization by affecting cell membrane permeability, subsequent root exudation, and final plant growth response, each of these in turn possibly influencing the development of a particular disease. Other elements also may be influential in mycorrhizae-disease interactions. Low concentrations of potassium in leaves of mycorrhizal cotton may have been the cause of increased severity of Verticillium wilt (Davis et al., 1979).

Results from Part 1 of this dissertation are interpreted to mean that mycorrhizae influenced the development of Fusarium wilt of tomato. The time to onset of disease symptoms was earlier in plants inoculated with either of two mycorrhizal fungi and the wilt fungus than plants inoculated with the wilt fungus alone. Eventually disease became severe in all plants inoculated with the wilt fungus. Disease was least severe

in plants inoculated with the wilt fungus alone plus PO_4 amendments, intermediate in plants inoculated with either mycorrhizal fungus plus the wilt fungus, and greatest in plants inoculated with the wilt fungus alone. Quantitative differences in nutrition in plants inoculated with either mycorrhizal fungus and/or the wilt fungus could explain the relative ranking of treatments.

The purpose of this study was to elucidate the effect of two species of mycorrhizal fungi and the Fusarium wilt fungus on elements in tissue of tomato. Data from Part 1 of this dissertation were interpreted to mean that growth response of tomato to each species of mycorrhizal fungi tested differed, therefore both species were evaluated for influences on nutrient contents.

Materials and Methods

Data reported herein were taken in conjuction with experiments described in Part 1 of this dissertation. Plants were harvested 8 wk after inoculation in the transplant and seed experiments (first performances of each experiment). Shoots from three replicate plants per fungus treatment were dried for 36 hr at 70 C. Each shoot was ground using a Wiley mill (20-mesh-sieve), and a subsample (250 mg) of each shoot was ashed in a Muffle furnace for 8 hr at 490 C. The ashed sample was digested in 0.1 N hydrochloric acid, passed through Whatman #42 filter paper, and the filtered solution was collected in an acid-washed glass vial. Analyses of samples by atomic absorption spectrophotometry for calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), and PO_4 were performed by the Soils Clinic, University of Florida, Gainesville.

Data were analyzed by analysis of variance and by Duncan's multiple range test. In that few significant linear relationships were detected between inoculum density and plant growth in the experiments from which these plants were obtained (see Results section, Part 2 of this dissertation), data were averaged over inoculum levels to improve the chances of detecting differences in total quantities and concentrations of elements between fungus treatments. Data are expressed as either the concentration of an element per g of shoot tissue:

µg element/ g dry weight shoot tissue ,

or as the total quantity of an element per plant:

(µg element/g dry weight shoot tissue) x

(µg dry weight shoot tissue/ plant).

Results

Results of nutrient contents in plants from each treatment differed according to the method used for comparisons; more differences between treatments were observed when treatments were compared for total quantities rather than concentrations of elements per plant. Total quantities, but not concentrations, of all elements were greatest in noninoculated plants receiving a PO_4 amendment and least in plants inoculated with the wilt fungus alone (Tables 34 and 35). Total quantities of elements decreased to a greater extent in plants inoculated dually with each mycorrhizal fungus and the wilt fungus compared with plants inoculated with each mycorrhizal fungus alone. This decrease occurred to a greater extent when transplants were inoculated compared with when seeds were inoculated.

Either mycorrhizal fungus increased nutrient contents compared with noninoculated plants more frequently when total quantities rather than concentrations of elements were considered (Tables 34 and 35). ever, amending noninoculated plants with PO_4 resulted in increased nutrient contents of shoots to levels above those in shoots from all other plants. This increase occurred when either transplants or seeds were inoculated. Similarly PO_4 amendments resulted in increased nutrient contents in plants inoculated with the wilt fungus alone. Generally nutrient contents in plants inoculated with the wilt fungus alone and amended with PO_4 did not exceed those in plants inoculated dually with either mycorrhizal fungus and the wilt fungus.

The two species of mycorrhizal fungi affected nutrient contents differently. In three out of four cases, the level of PO_4 was higher in plants inoculated with G. mosseae than in those inoculated with G.

etunicatum (Tables 34 and 35). The total quantity and concentration of K was greatest in plants inoculated with G. mosseae compared with G. etunicatum, and was least in plants inoculated dually with G. etunicatum plus the wilt fungus compared with G. mosseae plus the wilt fungus. Thus opposite results in nutrient contents of K were found between the two mycorrhizal fungi with respect to the presence of the wilt fungus.

Table 34. Effect of planting tomato (cv. Manapal) transplants in soil infested with either Glomus etunicatum (Ge) or G. mosseae (Gm) and/or with Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on elements in shoots, where data were collected from the first experimental performance

Treatment[t]	Ca[w,x]	Cu	Fe	K	Mg	Mn	PO_4	Disease severity[y] 6 wk	8 wk
Concentration (µg/ g tissue)[u]									
Noninoculated	236.7 a[z]	0.09 c	0.47 b	453.3 c	94.7 ab	4.47 a	38.0 c	0.00 b	0.00 b
Noninoculated + PO_4	278.3 a	0.10 c	0.90 ab	476.7 bc	106.3 ab	4.33 a	54.2 bc	0.00 b	0.00 b
Ge	246.3 a	0.11 c	0.75 ab	465.0 c	102.0 ab	4.89 a	39.7 c	0.00 b	0.27 b
Gm	236.2 a	0.12 bc	0.60 b	533.3 bc	85.0 b	4.41 a	47.2 bc	0.00 b	0.00 b
Ge + Fol	323.2 a	0.20 a	1.16 a	736.7 a	124.7 a	5.21 a	91.2 a	2.57 a	3.73 a
Gm + Fol	305.4 a	0.20 a	1.20 a	666.7 ab	112.2 ab	4.69 a	100.7 a	2.73 a	3.93 a
Fol	263.3 a	0.23 a	1.03 ab	656.7 ab	94.7 ab	4.83 a	97.3 a	2.60 a	4.00 a
Fol + PO_4	207.7 a	0.18 ab	0.73 ab	886.7 a	98.7 ab	4.30 a	77.5 ab	2.20 a	4.00 a
Quantity (µg/ plant)[v]									
Noninoculated	781.8 bc	0.29 a	1.30 c	1512.4 bcd	310.8 bc	13.94 ab	136.8 b	0.00 b	0.00 b
Noninoculated + PO_4	1324.0 a	0.47 a	3.29 a	2212.3 a	482.8 a	18.12 a	259.4 a	0.00 b	0.00 b
Ge	827.7 b	0.36 a	2.52 ab	1628.0 bc	365.2 b	17.00 a	153.6 b	0.00 b	0.00 b
Gm	787.5 bc	0.39 a	2.25 abc	1803.4 ab	288.1 c	15.75 a	151.6 b	0.00 b	0.00 b
Ge + Fol	636.9 cd	0.38 a	2.06 bc	1369.0 cde	227.8 cd	9.72 c	163.9 b	2.57 a	3.73 a
Gm + Fol	517.1 de	0.33 a	1.99 bc	1134.9 de	184.1 de	7.93 c	169.7 b	2.72 a	3.93 a
Fol	289.3 e	0.23 a	1.08 c	759.7 e	106.9 e	5.04 c	106.9 b	2.60 a	4.00 a
Fol + PO_4	461.8 de	0.42 a	1.83 bc	2071.0 ab	224.0 cde	10.01 bc	162.0 b	2.20 a	4.00 a

[t] Plants grown in noninfested soil (noninoculated [PO_4, phosphorus]) or grown in soil infested with Ge or Gm at 0.1, 0.5, and 1.0 chlamydospore per gram dry soil (cpg) and/or with Fol (+ PO_4) at 500 cpg; data averaged over inoculum levels of each mycorrhizal fungus.

[u] Concentration of each element per plant was calculated as follows: µg element/gram dry weight shoot tissue.

[v]Total quantity of each element per plant was calculated as follows: ([µg element/gram dry weight shoot tissue] x [µg dry weight shoot tissue/plant]).

[w]Quantified elements: calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), and PO_4.

[x]Data collected at 8 wk after infestation unless noted otherwise; each value represents the mean of either three or nine replicates for nonmycorrhizal or mycorrhizal treatments, respectively, unless noted otherwise.

[y]Data collected 6 and 8 wk after transplanting into infested soil; each value represents the mean of either five or fifteen replicates for nonmycorrhizal or mycorrhizal treatments, respectively.

[z]Numbers in the same column followed by the same letter do not differ significantly ($P < 0.05$) by Duncan's multiple range test.

Table 35. Effects of planting tomato (cv. Manapal) seeds in soil infested with either Glomus etunicatum (Ge) or G. mosseae (Gm) and/or with Fusarium oxysporum f. sp. lycopersici race 2 (Fol) on elements in shoots, where data were collected from the first experimental performance

Treatment[t]	Ca[w,x]	Cu	Fe	K	Mg	Mn	PO_4	Disease severity[y] 6 wk	8 wk
Concentration (µg/ g tissue)[u]									
Noninoculated	380.0 a[z]	0.21 ab	1.20 ab	606.7 a	72.0 ab	4.03 a	63.7 ab	0.00 c	1.60 b
Noninoculated + PO_4	386.7 a	0.25 a	1.77 a	723.3 a	81.7 ab	4.47 a	67.8 a	0.00 c	1.60 b
Ge	252.5 c	0.18 ab	0.70 bc	631.3 a	70.6 b	3.54 a	47.8 b	0.07 c	1.40 b
Gm	262.1 bc	0.19 ab	0.90 b	671.1 a	88.6 a	4.14 a	67.3 a	0.13 c	1.53 b
Ge + Fol	328.3 ab	0.19 ab	0.79 bc	707.8 a	79.9 ab	4.24 a	58.4 ab	0.87 b	2.60 a
Gm + Fol	312.2 abc	0.17 b	0.42 c	605.6 a	78.4 ab	3.67 a	49.9 ab	1.50 a	2.77 a
Fol	281.7 abc	0.19 ab	0.60 bc	593.3 a	62.0 b	3.70 a	61.2 ab	1.60 a	2.80 a
Fol + PO_4	305.0 abc	0.21 ab	0.57 bc	596.7 a	73.7 ab	4.37 a	63.8 ab	1.00 ab	2.60 a
Quantity (µg/ plant)[v]									
Noninoculated	1041.7 b	0.55 b	3.58 b	1607.4 abc	195.7 a	11.73 ab	167.2 ab	0.00 c	1.60 b
Noninoculated + PO_4	1164.4 a	0.75 a	5.96 a	2184.2 a	246.1 a	13.89 a	207.8 a	0.00 c	1.60 b
Ge	668.7 e	0.49 b	2.22 cd	1702.2 ab	183.4 a	10.03 abc	129.5 b	0.07 c	1.40 b
Gm	764.8 cd	0.54 b	2.65 bc	1956.9 a	260.0 a	12.22 ab	195.7 a	0.13 c	1.53 b
Ge + Fol	818.9 c	0.45 bc	1.78 cd	1706.1 ab	208.9 a	9.83 abc	133.7 b	0.87 b	2.60 a
Gm + Fol	734.2 d	0.40 bc	0.84 f	1405.6 bc	207.2 a	9.50 bc	133.3 b	1.50 a	2.77 a
Fol	474.1 f	0.32 c	0.92 ef	1060.4 c	108.5 a	6.23 c	114.7 b	1.60 a	2.80 a
Fol + PO_4	653.1 e	0.38 bc	0.97 ef	1264.2 bc	147.4 a	8.98 bc	126.1 b	1.00 ab	2.60 a

[t]Plants grown in noninfested soil (noninoculated [PO_4, phosphorus]) or grown in soil infested with Ge or Gm at 0.1, 0.5, and 1.0 chlamydospore per gram dry soil (cpg) and/or with Fol (+ PO_4) at 500 cpg; data averaged over inoculum levels of each mycorrhizal fungus.

[u]Concentration of each element per plant was calculated as follows: µg element/gram dry weight shoot tissue.

[v] Total quantity of each element per plant was calculated as follows: ([µg element/gram dry weight shoot tissue] x [µg dry weight shoot tissue/plant]).

[w] Quantified elements: calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), and PO_4.

[x] Data collected 8 wk after infestation unless noted otherwise; each value represents the mean of either three or nine replicates for nonmycorrhizal or mycorrhizal treatments, respectively, unless noted otherwise.

[y] Data collected 6 and 8 wk after infestation; each value represents the mean of either five or fifteen replicates for nonmycorrhizal or mycorrhizal treatments, respectively.

[z] Numbers in the same column followed by the same letter do not differ significantly ($P < 0.05$) by Duncan's multiple range test.

Discussion

Apparently the PO_4 amendment was sufficient to raise the level of PO_4 and all other nutrients in noninoculated plants to levels (both total quantity and concentration) which were equivalent to or higher than levels in plants in all other treatments. The higher levels of PO_4 may indicate that either the increase in PO_4 uptake in mycorrhizal plants was not as great as would be expected, or that individual mycorrhizal fungus colonization sites, compared with the spread of the mycorrhizal fungus in the root cortex (refer to Parts 1 and 2 of this dissertation for a discussion of mycorrhizal fungus development in the root system of tomato), were insufficient to provide improved PO_4-uptake.

Whereas improved phosphorus nutrition has been accepted as the factor responsible for improved growth in mycorrhizal plants, PO_4 has not been implicated consistently as being the important factor determining the influence of mycorrhizal fungi on plant growth in disease interactions involving mycorrhizal fungi. Phosphorus levels (as well as levels of other nutrients) were lower in plants inoculated with the wilt fungus alone compared with all other plants. These results can support the conclusions of results on these same experiments described in Part 1 of this dissertation. Disease severity 8 wk after inoculation was greatest in plants inoculated with the wilt fungus alone, intermediate in plants inoculated with a mycorrhizal fungus and the wilt fungus, and least in those inoculated with the wilt fungus where PO_4 was amended. Insufficient PO_4 concentrations may have made the plants more susceptible to disease.

Plant and soil concentrations of K and Fe are thought to be involved in the development of Fusarium wilt of tomato. Walker and Foster (1946)

reported that plants inoculated with the wilt fungus and grown in low-K soil were more susceptible to wilt than were inoculated plants grown in high-K soil. Tissue analyses were not presented in their study, therefore an assumption must be made regarding a direct correlation between concentrations (or total quantities of elements) in plants and in soil. Potassium may be involved in the mechanism of resistance in tomato to Fusarium wilt. Plants inoculated with both the wilt fungus and a mycorrhizal fungus had higher (not significant) levels of K and Fe compared with plants inoculated with the pathogen alone. Levels of Fe below a threshold are thought to lessen the severity of Fusarium wilt development, as the pathogen has a high Fe requirement for growth and sporulation (Jones and Woltz, 1972). It is possible that by 8 wk after inoculation (when data were collected), the nutritional status (other than K or Fe) of plants inoculated with a mycorrhizal fungus generally had improved sufficiently to provide some compensation to the plant reducing disease expression.

Explanations for the earlier time of onset of disease symptoms are incomplete. Possibly either hormones or root exudates may have been affected, thereby influencing the activities of the pathogen and/or the mycorrhizal fungi. In that the differences between treatments in disease severity at the time of the assay were minimal, conclusions regarding nutrient-mediated effects on the mycorrhizae-disease interaction are likely to be incomplete.

Maintaining a high level of PO_4 both external and internal to the plant or using the mycorrhizal fungus G. mosseae, may reduce disease expression in Fusarium wilt of tomato. Nutrient contents were greater in plants which received PO_4 amendments, and in plants inoculated with

G. mosseae than in plants inoculated with G. etunicatum with or without the wilt fungus. Further work is needed to clarify the mechanisms by which the development of Fusarium wilt of tomato is influenced by nutrients in the soil and plant by mycorrhizal fungi.

APPENDIX 4

THE RELATIONSHIP OF INOCULUM DENSITY OF *FUSARIUM OXYSPORUM* F. SP. *LYCOPERSICI* TO DISEASE INCIDENCE AND INFECTION INCIDENCE IN TOMATO

Introduction

The relationships of inoculum density (ID) to disease incidence (DI) or infection incidence (InfI) have been quantified for a number of diseases caused by soilborne plant pathogenic fungi (Baker, 1971; Vanderplank, 1975); however, these relationships have never been quantified for Fusarium wilt of tomato. Welch and Schneider (1980) reported that less than a single propagule per gram of air-dry soil resulted in incidence of Fusarium yellows of celery under field conditions, and that greater disease severity (DS) was associated with higher initial inoculum loads. Similarly Nyvall and Haglund (1972) found that a single infection site by the Fusarium wilt fungus could result in the death of a pea plant, and that the severity of disease symptoms was directly proportional to the number of root and cotyledon infection sites. A greater susceptibility of young (less than 4-wk-old) plants to Fusarium yellows of celery was presumed to be related to the saturation of available infection sites when celery seedlings were transplanted into infested soil (Hart and Endo, 1981).

The method of inoculation of the pathogen has been shown to influence subsequent development of a disease caused by the Fusarium wilt fungus. Hart and Endo (1981) indicated that using a soil infestation

method of inoculation resulted in a greater amount of disease compared with a root-dip method because new roots could not outgrow the pathogen as would be possible using the root-dip method.

The objectives of this research were to establish procedures for inoculating tomato plants with chlamydospores, a propagule considered as the primary survival unit for other Fusarium spp. according to Nash et al. (1961), of Fusarium oxysporum Schlecht. f. sp. lycopersici (Sacc.) Snyd. & Hans. Additionally the relationship of ID of the wilt fungus to DI and InfI was studied to obtain information pertinant to Part 1 of this dissertation. Levels of inoculum of the wilt fungus used in Part 1 of this dissertation were based on the preliminary results obtained in this study.

Materials and Methods

The isolates used in this study were one isolate each of race 1 and 2 of F. oxysporum f. sp. lycopersici (Fol) collected from diseased tomato plants in 1977, and obtained from J. P. Jones, University of Florida Agricultural Research and Education Center, Bradenton. A single-spore culture of each isolate was maintained in a sterilized mixture of soil and sand (1/1, v/v) at 5 C. All materials and methods utilized in this study for chlamydospore production, soil infestation, and seeding were identical with those described in Part 1 of this dissertation, with the exception that a 10.2-cm-diameter clay pot was used as the plant growth container.

In that subsequent studies (described in Part 1 of this dissertation) were to be conducted using the ID from this experiment selected to result in 50% DI or InfI (ID_{50}, Inf_{50}) at 6-8 wk after inoculation, relatively low levels were selected to inoculate tomato (Lycopersicon esculentum Mill. 'Manapal'): 50, 100, 500, and 1000 chlamydospores per g of soil (cpg). Soil populations were evaluated at 0 and 24 hr, and 18, 38, 60, and 108 days after infestation. Soil propagule population densities from each pot containing a plant were enumerated using the procedures and methods described in Part 1 of this dissertation. Two selective media were compared for efficiency in assaying population densities of F. oxysporum: 1) PCNB medium described in Part 1 of this dissertation; and 2) Komada's medium (Komada, 1975).

Root infection incidence (RInfI), and the distribution of root and stem infections were monitored 18, 38, and 60 days after inoculation. All incidence data were based on the percent of plants (DI) or root systems (RInfI) in a population of five with disease symptoms or

evidence of infection for DI and RInfI, respectively. To determine RInfI and the distribution of infection in roots of each plant, each root system (with roots oriented in parallel alignment) was cut at 2.5-cm-interval distances from the crown, and a single segment representing each interval was plated on selective medium using the methods and media described in Part 1 of this dissertation. The presence or absence of infection by F. oxysporum in each segment was recorded. Each segment represented an increasing distance from the root crown, and a root system was considered to be infected if F. oxysporum was recovered from any segment of that root system.

The distribution of infection in each stem was determined by excising a 1-cm-long stem segment at each 10-cm distance from the crown, surface-disinfecting segments in 0.525% sodium hypochlorite for 2 min, rinsing in sterile deionized water, and plating on pentachloro-nitro-benzene (PCNB) medium. Plates were incubated at 25 C for 7-10 days and stem segments were evaluated for the presence or absence of F. oxysporum. There were five plant replicates per treatment and the experiment was performed once.

Results

Comparisons are presented in Table 36 for the relative efficiency of the two selective media for purposes of assaying F. oxysporum. Since results of comparisons were similar at each assay, the data presented were taken from the assay at 108 days after infestation. The numbers of propagules per gram of dry soil (ppg) recovered were greater using PCNB compared with Komada's medium at each inoculum level, except at 50 cpg for race 2. Since PCNB apparently was superior or similar to Komada's medium, PCNB was used for subsequent assays.

The relationship of the initial ID to the soil propagule population densities enumerated on PCNB medium is presented for soil infested with either race 1 or race 2 (Fig. 5). In general populations in soil infested with race 1 did not differ (except for populations associated with 100 cpg at 60 days after infestation) regardless of initial levels of infestation. At each assay a greater number of propagules were counted when soil was infested with race 2 compared with race 1. The relationship of the population recovered to initial ID differed for each race. For soil infested with race 2, populations increased sharply in the first 24 hr after infestation and continued to increase through 18 and 38 days after infestation for each inoculum level. The relative ranking of initial inoculum levels was maintained for enumerated populations at the 24-hr, and 18-day assays. At the 60-day assay, populations in soil infested with race 2 at 100 cpg had increased to a level above that of other inoculum levels. Maximum populations (13,340 ppg) occurred at 1000 cpg 38 days after infestation. Populations at each ID declined after the 38-day assay, and by 108 days after infestation, populations were around 4000 ppg for the 500- and 1000-cpg levels, and

200 ppg for the 50- and 100-cpg levels. Thus while populations tended to increase for both isolates in the first 24 hr, generally populations did not increase further in soil infested with race 1, whereas populations continued to increase in soil infested with race 2 for the first 38 days after infestation and declined thereafter.

Populations of F. oxysporum occurred in noninfested soils. Generally the increase in populations was delayed but followed the same pattern of development as for populations in soil infested with race 2.

Infection levels increased rapidly between the 18- and 38-day assay, and by 60 days 100% RInfI was found for a majority of inoculum levels for both isolates (Fig. 6). In plants grown in soil infested with race 1, the highest and lowest RInfI values occurred at 50 and 500 cpg, respectively, at the 18-day assay. In contrast in plants grown in soil infested with race 2, the highest and lowest RInfI values occurred at 500 and 100 cpg, respectively. Values of 100% RInfI were reached at 38 and 60 days after infestation in soil infested with race 2 and race 1, respectively.

In soil infested with race 2, the greatest DI values occurred at 500 cpg at the 38-day assay (Table 37). Disease incidence tended to increase with increasing inoculum levels in soil infested with races 1 and 2. The distribution of root infection became more extensive with increased time after infestation and was similar for the two races at all sampling dates (Table 38). The distribution of stem infection also became more extensive with increased time after infestation, but the wilt fungus was isolated more frequently from stem sections of plants grown in soil infested with race 2 compared with race 1 at all sampling dates. The maximum height above the crown from which the wilt fungus was isolated

increased with time after inoculation when race 2 was used, and this distance reached over 80 cm in one inoculum level at the 60-day assay. Stem infections were not observed in plants grown in noninfested soil. Some root infection occurred in plants grown in noninfested soil; however, this was observed only at the 60-day assay, and the distribution of infection was less extensive than that observed in plants grown in soil infested with either race of the pathogen.

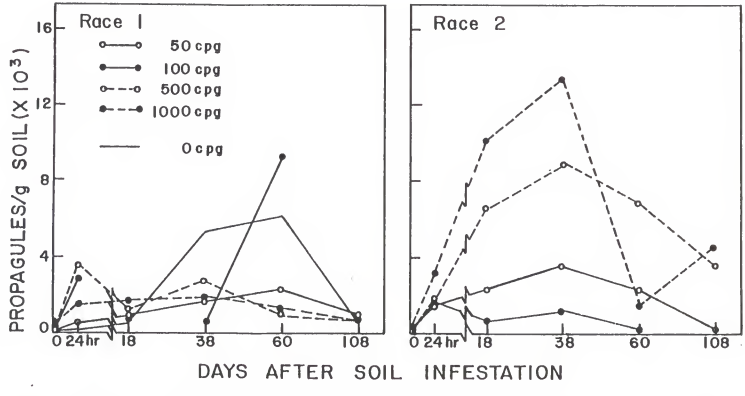

Fig. 5. The relationship of propagule population densities of Fusarium oxysporum under greenhouse conditions to time at five initial densities of chlamydospores of either race 1 or race 2 of F. oxysporum f. sp. lycopersici in autoclaved soil where tomato plants (cultivar Manapal, resistant or susceptible to races 1 and 2, respectively) were grown. Initial chlamydospore densities per gram dry soil = cpg, and noninfested soil = 0 cpg.

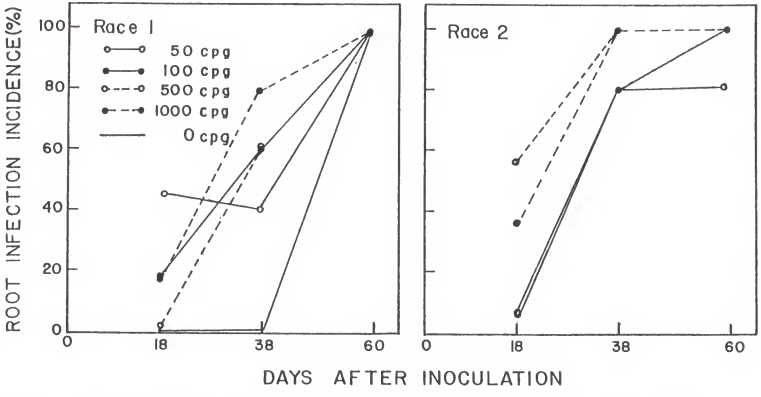

Fig. 6. The relationship of percentages of root systems of tomato (cultivar Manapal, resistant or susceptible to races 1 and 2, respectively, of the wilt fungus) plants infected with the wilt fungus under greenhouse conditions to time at five initial densities of chlamydospores of either race 1 or race 2 of Fusarium oxysporum f. sp. lycopersici per gram autoclaved dry soil (cpg). Noninfested soil = 0 cpg.

Table 36. Soil propagule population densities of Fusarium oxysporum recovered 108 days after infestation of autoclaved soil with the wilt fungus and growth of the tomato cultivar Manapal (resistant or susceptible to races 1 and 2, respectively)

Inoculant[x]	ID (cpg)[y]	Selective medium	
		Komada's	PCNB
Race 1	50 cpg	844[z]	978
Race 1	500 cpg	267	689
Race 1	1000 cpg	578	578
Race 2	50 cpg	533	222
Race 2	500 cpg	1889	3556
Race 2	1000 cpg	1889	4556

[x] A single isolate of either race 1 or 2 of F. oxysporum f. sp. lycopersici were used as the inoculants.

[y] Chlamydospores used as inoculum, where initial inoculum density (ID) = chlamydospores per gram dry soil (cpg).

[z] Based on 1:200 soil dilutions, two replicate plates per ID x race combination (five plates/replicate), and incubation of plates at 25 C for 7-10 days.

Table 37. The influence of planting tomato (cv. Manapal, resistant or susceptible to races 1 and 2, respectively, of the wilt fungus) in noninfested soil or in soil infested with either race 1 or 2 of the wilt fungus on disease incidence

Inoculant[x]	Disease incidence (%)				
	0 cpg	50 cpg[y]	100 cpg	500 cpg	1000 cpg
Race 1	0.0	0.0	7.1[z]	5.9	0.0
Race 2	0.0	16.7	30.5	35.3	19.0

[x]A single isolate of either race 1 or 2 of Fusarium oxysporum f. sp. lycopersici were used as the inoculants.

[y]Initial number of chlamydospores per gram dry soil (cpg) used to infest autoclaved soil.

[z]Based on percent of five plants per inoculum level x race combination with shoot disease symptoms of chlorosis and wilt.

Table 38. Distribution of infection in stems and roots of the tomato cultivar Manapal (resistant or susceptible to race 1 and race 2, respectively) grown in noninfested soil or soil infested with Fusarium oxysporum f. sp. lycopersici

ID[u]	Percent Rinf1[v]	Infection distance (cm)[w] Isolated from root[x] 2.5	5.0	7.5	10.0	12.5	Isolated from shoot[y] 10	20	30	40	50
18 days after infestation											
Race 1											
50 cpg	45	+	+	+	-	-	+	-	-	-	-
100cpg	18	+	-	-	+	-	-	-	-	-	-
500 cpg	0	-	-	-	-	-	-	-	-	-	-
1000 cpg	17	-	+	+	-	-	-	-	-	-	-
Race 2											
50 cpg	6	-	-	-	+	-	-	-	-	-	-
100 cpg	3	+	+	+	+	-	+	-	-	-	-
500 cpg	56	+	+	-	-	-	+	+	-	-	-
1000 cpg	36	+	+	+	+	-	+	-	-	-	-
Noninfested (0 cpg)	0	-	-	-	-	-	-	-	-	-	-
38 days after infestation											
Race 1											
50 cpg	40	+	+	+	+	-	+	-	-	-	-
100 cpg	60	+	+	-	+	-	-	-	-	-	-
500 cpg	60	+	-	+	-	-	-	-	-	-	-
1000 cpg	80	+	-	-	+	+*[z]	-	-	-	-	-
Race 2											
50 cpg	80	+	+	+	-	+*,*	+	+	+	-	+*
100 cpg	80	+	+	+	+	-	+	+	+	+	-
500 cpg	100	+	-	+	+	-	+	+	+	+	-
1000 cpg	100	+	+	+	+	-	+	+	+	+	-
Noninfested (0 cpg)	0	-	-	-	-	-	-	-	-	-	-

60 days after infestation

Race 1											
50 cpg	100	+	+	+	+	+*	+	+	-	-	-
100 cpg	100	+	+	+	+	+	+	-	-	-	-
500 cpg	100	+	+	+	+	+	-	-	-	-	-
1000 cpg	100	+	+	+	+	+	-	-	-	-	-
Race 2											
50 cpg	80	+	+	+	+	+	+	+	+	+	+*
100 cpg	100	+	+	+	+	+	+	+	+	+	+
500 cpg	100	+	+	+	+	+	+	+	+	+	-
1000 cpg	100	+	+	+	+	+*,*	+	+	+	+	+*,*,*
Noninfested (0 cpg)	100	-	-	+	+	+	-	-	-	-	-

[u]Initial inoculum density (ID) of chlamydospores per gram dry soil (cpg) of either isolate of race 1 or 2 in autoclaved soil.

[v]Based on proportion of five five plants per ID x race combination where roots were infected by the wilt fungus.

[w]Roots and shoots excised from whole plants at increasing distances of 2.5-cm- (root) or 10-cm-(shoot) intervals from the crown and plated on selective PCNB medium.

[x,y]Based on the presence (+) or absence (-) of infection in each sequential root or shoot section away from crown.

[z]* Indicates distances (in increments of 2.5- or 10-cm for root systems or shoots, respectively) beyond 12.5-cm- or 50-cm-distances from crown for roots or shoots, respectively from which the wilt fungus was isolated.

Discussion

Both isolates had penetrated and infected the root systems at 18 days after infestation. Root infection probably occurred earlier, but plants were not assayed at less than 18 days after infestation. The distribution and extent of root infection was similar for both isolates at all assays. Race 2 infected stem tissue to a greater extent. These data support the contention by Snyder and coworkers (1946) and others (Conway and MacHardy, 1978; Scheffer and Walker, 1954) that the mechanism of resistance in tomato to Fusarium wilt may not be governed by physical barriers in the host's root system. Conway and MacHardy (1978) reported findings similar to those presented in this study; limited and extensive distribution of infections in stems were found in resistant and susceptible wilt fungus x host combinations, respectively. They suggested that the virulence of race 2 toward a susceptible cultivar is related to its capacity to overcome the resistance mechanism that normally localizes infections. In the experiments reported herein, the resistance mechanism of the tomato cultivar Manapal to race 1 may have prevented large increases in soil populations by limiting extensiveness of root infections. In contrast in the absence of a localization phenomenon, the successful spread of race 2 through root and stem tissue may have occurred, thus allowing sustained increases in soil populations. Further studies should be conducted to evaluate quantitatively the distribution and spread of races 1 and 2 in root systems of susceptible and resistant tomato cultivars.

The activity (root and stem infection and soil populations) of race 2 was related to ID more frequently than was the activity of race 1. The relative increases in the number of recoverable propagules and DI as functions of increasing ID occurred only in soil infested with

race 2. The highest RInfI and DI achieved occurred sooner in soil infested with race 2 compared with race 1.

An ID_{50} for 50% InfI at 6-8 wk after inoculation was difficult to obtain in that RInfI reached 100% by 38 days after infestation. Therefore the ID_{50} which resulted in a DI closest to 50% at 38 days after infestation (500 cpg of race 2; Table 2) was selected for future experimental use.

The occurrence of consistent relationships between ID and soil propagule population densities, infection incidence or DI in soil infested with race 2 indicates that inoculum density is an important factor in the epidemiology of Fusarium wilt of tomato.

APPENDIX 5

GENERAL CONCLUSIONS

Quantitative relationships exist between increasing levels of spore inoculum of vesicular-arbuscular mycorrhizal fungi and fungus development. However, inconsistent effects on host growth were obtained by raising the inoculum level from 0.1 to 10.0 chlamydospores of Glomus etunicatum and G. mosseae per gram of dry soil (cpg). Inoculation of tomato (Lycopersicon esculentum) plants with either of the mycorrhizal fungus species and the Fusarium wilt fungus (Fusarium oxysporum f. sp. lycopersici resulted in earlier time to disease onset than in plants inoculated with the wilt fungus alone. Eventually disease became more severe in plants inoculated with the wilt fungus alone than in plants inoculated with a mycorrhizal fungus and the wilt fungus. Raising the spore inoculum level from 0.1 to 1.0 cpg did not effect subsequent disease development consistently. Experimental conditions are suggested as being of primary importance in influencing the development of the mycorrhizal fungi and wilt fungus in the host and the subsequent effects on plant growth and disease development.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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